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STUDIES ON ASAPHES FLETCHERI (CRAWFORD), A HYPERPARASITE OF APHIDIUS TESTACEIPES (CRESSON) AND PRAON AGUTI (SMITH), PRIMARY PARASITES OF APHIDS[1]

P. S. SEKHAR

ABSTRACT

This pteromalid hymenopteron was cultured on both the braconid species named above. Mating was preceded by courtship. This began, on the average, 68 minutes after emergence, continued for about four minutes, and was followed by copulation which required about 15 seconds. Each male was capable of mating with more than one female, but mated females were completely unattractive to males. Fertilized females produced mostly female progeny, unmated ones only males, and the progeny of the unmated ones were fewer than those of mated females. Though generally ready for oviposition as soon as they dried after emergence, if females were mated there was an interval of about 45 minutes before oviposition was begun; however, if suitable hosts were available to them, newly emerged females did not court or mate but proceeded with oviposition. Deposition of an egg consumed about six minutes. The total period of oviposition per female ranged from 2 to 13 days when they were allowed to attack 2 hours per day; the maximum number of attacks occurred on the first day, and ovipositional attacks were most numerous at 28° C. The life cycle from egg to adult required a maximum of about 27 days at 23° C. and a saturation deficiency of 3 mm., and a minimum of about 10 days at 30° and a saturation deficiency of 8 mm. Males completed this cycle more rapidly than females, but adult females lived longer than adult males. Marked discrimination was shown in selecting hosts. Only dead, sessile, parasitized aphids were chosen for attack. The early pupae of *A. testaceipes*, contained in such aphids, were preferred to late larvae, but with *P. aguti* the late larvae were more frequently attacked than the pupae. On the whole, a greater percentage of hyperparasitism was accomplished on *Aphidius testaceipes* than on *Praon aguti*; and in the field an increase in the population of *Asaphes fletcheri* was seen to bring about a marked scarcity of *A. testaceipes*, especially in one locality where both this species and *P. aguti* were present.

INTRODUCTION

In the summer of 1954 the author observed a high degree of mortality in test populations of the braconid *Aphidius testaceipes* (Cresson) in one of the greenhouses of the University of Massachusetts. Laboratory studies showed that this was due chiefly to attacks of *Asaphes fletcheri* (Crawford) (Hymenoptera, Pteromalidae) upon this parasite of aphids. Further investigations, both indoors and outdoors, revealed that *A. fletcheri* also attacks *Praon aguti* (Smith), another braconid parasite of aphids. This latter species has not previously been listed among its hosts.

Though the problems created by the presence of *Asaphes fletcheri* hampered the progress of studies on *A. testaceipes*, they opened new fields for investigation. One new problem was to increase our knowledge of the relationships of *A. fletcheri* with the host *A. testaceipes*. Another was to discover the nature of the host relationships with *Praon aguti*. A third was to determine whether the hyperparasite showed any degree of preferential discrimination between these two hosts, and, further, between different developmental stages of either of them. Observations on the habits of *Asaphes fletcheri* and on the influence of certain ecological factors on its life history have also been recorded. It is hoped that the information presented here may aid in analyzing the nature of its host relationships, particularly in the light of a statement which has been made that hyperparasites are less discriminating than primary parasites in the selection of hosts.

REVIEW OF LITERATURE

Past contributions on the hyperparasite *Asaphes fletcheri* are scanty. First described as *Megorismus fletcheri* by Crawford (1909), it was transferred to the genus *Asaphes* by Peck (1951). Recently Burks (1954, in correspondence) has stated that *Asaphes americana* Girault, 1914, is a synonym of *A. fletcheri*. As recorded by Peck, partly under *A. americana* and partly under *A. fletcheri*, its range in North America extends from

[1]Part of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Massachusetts, Amherst, Mass. Accepted for publication April 20, 1957.

Iowa and Wisconsin through Ontario and Quebec to New York and Connecticut, and south to Kentucky and North Carolina. Massachusetts is now added to the list of localities.

There are many aphids, as well as *A. testaceipes* and other primary parasites, in the list of hosts recorded for *Asaphes fletcheri*. The listing of aphids as primary hosts suggests that *A. fletcheri* may indeed act as a primary parasite, but it seems probable that such listings have resulted from failure to recognize exact sequences of parasitic attack.

Recorded knowledge of the biology of *Asaphes fletcheri* is very limited. Spencer (1926) and Griswold (1929) have presented information on the habits and biology of the species, and Griswold also described and figured the immature stages.

Economic Importance.—The literature contains no statistical data to show the extent of hyperparasitization by *Asaphes fletcheri* on the primary parasites *Aphidius testaceipes* and *Praon aguti*. Nevertheless, reports of the occurrence of this hyperparasite in various regions warrant careful investigation. Griswold (1929) suggested that *A. fletcheri* may act as either a secondary or a tertiary parasite, depending upon circumstances. In the latter event, and if preference is shown for other secondary parasites (such as *Charipes* sp., which is a secondary parasite on *Aphidius* sp.), then *Asaphes fletcheri* could be considered beneficial.

MATERIAL AND METHODS

Aphids and Primary Parasites.—Specimens of various aphid hosts and of their primary parasites, *Aphidius testaceipes* and *Praon aguti*, were procured from several localities on the campus of the University of Massachusetts. Steady populations of the two primary parasites were maintained in the laboratory on cultures of their respective hosts, reared on food plants suitable for each. Thus *A. testaceipes* was cultured on cotton aphis (*Aphis gossypii* Glover) colonized on squash (*Cucurbita* sp.), while *P. aguti* was cultured on rose aphis (*Macrosiphum rosae* L.) colonized on rose (*Rosa* sp.). The rearing techniques described by Smith (1944) were found satisfactory.

Hyperparasites.—Specimens of *Asaphes fletcheri* were obtained from the campus localities by two methods: (1) sweeping with a hand net for the adults, and (2) collecting hyperparasites in the laboratory from material obtained outdoors.

The primary parasites were identified by Dr. C. F. W. Muesebeck, and the hyperparasites by Dr. B. D. Burks, of the U. S. National Museum.

Rearing.—Mass rearing of the hyperparasites on the immature stages of *Aphidius testaceipes* was conducted in cages in the laboratory and greenhouse attached to the Department of Entomology. Only a limited number of *A. fletcheri* were successfully reared from *Praon aguti*. After hyperparasitization was accomplished, the primary aphid host was transferred from the plant into a small bottle, and was kept at uniform temperature and humidity.

The moisture in the sealed rearing jars was controlled with saturated salt solutions. Three saturation deficiencies, 3 mm., 8 mm., and 15 mm., were maintained at each of the three temperatures, 23°, 27°, and 30° C., respectively. Table 1 lists the salts used to obtain these saturation deficiencies at the various experimental temperatures.

TABLE 1

SATURATION DEFICIENCIES EMPLOYED AND SALTS USED TO OBTAIN THEM

TEMPERATURE, °C.	SATURATION DEFICIENCY, APPROXIMATE (MM. OF MERCURY)	SALT
23	3	Potassium chloride
	8	Ammonium nitrate
	15	Magnesium chloride
27	3	Sodium potassium tartrate
	8	Potassium tartrate
	15	Cobalt chloride
30	3	Copper chloride
	8	Sodium nitrate
	15	Sodium nitrite

Constant temperature chambers were used for the experiments at 27° and 30° C. The 23° temperature was maintained with a circulating water bath, which provided jar temperatures of 23°±0.8°.

The hyperparasites were fed on dilute solutions of sugar in water. The method of administering the food was that described by Holloway (1913), which was found satisfactory.

For studies on oviposition, the required temperatures were sustained by using electric lamps of different capacities, fitted into a rectangular chamber. The chamber was made up of a wooden frame with cardboard screens covering its sides and an opaque glass plate covering its top. A jar cage, enclosing dead aphids containing the primary parasites, was placed over the opaque plate and hyperparasites were then admitted to this cage. Adequate care was exercised to keep the temperature in the cage nearly constant (±0.5° C.). Humidity levels were adjusted by varying the water surface area through the use of vials of different sizes in the cages. This arrangement was satisfactory also for studies in host relationships.

HABITS OF THE HYPERPARASITE *Asaphes fletcheri*

Mating.—Courtship and mating habits were studied by observation of 50 newly emerged pairs.

Of these, 15 pairs failed to court or mate throughout their lives, and six pairs courted intermittently but did not mate. In the 29 pairs observed to mate, courship began on the average 68 minutes after emergence, and lasted four minutes prior to copulation. These observations confirmed the statement of Griswold (1929) that courtship precedes mating. However, since she did not observe mating, her interpretation of what constitutes courtship may have been in error.

During the act of courtship the male exhibited movements of his antennae and wings. He stood face to face with the female and began tapping her antennae with his. At times he circled around to take a position behind her and touched her abdomen with his antennae. Meanwhile the female remained passive except for slight movements of the antennae. Then, after a brief pause in the activity of both sexes, the male jumped on the back of the female, grasping the sides of her body with his hind pair of legs, the middle pair resting on her wings, and the fore pair clasping her head from the sides. The female frequently fluttered her wings slowly before raising her abdomen to meet that of the male in copulation. In the mating pairs observed the average duration of copulation was about 15 seconds. Often two or three males were seen courting a single female simultaneously. Usually the first male to mount the female succeeded in mating with her. In one instance, however, a male which climbed on a female soon after another male had established himself was able to dislodge his predecessor and to perform copulation.

TABLE 2

Sex Ratio of the Progency Produced by Four Pairs and Four Unmated Females of *A. fletcheri*

	Number and Sex of Progeny			
	Mated		Unmated	
	Males	Females	Males	Females
	12	60	50	0
	2	88	58	0
	11	49	66	0
	10	53	37	0
Totals	35	250	211	0
Weighted percentage of sexes	12.2	87.7	100	0

Males are capable of mating with more than one female. How many times a female may mate in nature during her lifetime is unknown; in the laboratory a successfully mated female was no longer attractive to males. Mated females gave forth a majority of female progeny, while unmated females produced only males. It was noted also that unmated females produced fewer progeny than did mated females (Table 2).

Oviposition.—In general, females of *Asaphes fletcheri* were ready for oviposition as soon as they became dry after emergence. Mating was not a prerequisite to oviposition, but with mated females, on an average, some 45 minutes elapsed between the culmination of mating and the beginning of oviposition. If a newly emerged pair was enclosed with parasitized aphids which had turned brown, the female *Asaphes* did not respond to courting but proceeded with oviposition. However, the female responded immediately to the courting approaches of the male if the pair was kept together with no access to any hosts, or with access either to living aphids or to aphids that had not yet turned brown though they enclosed the developing larvae of the primary parasite.

The process of oviposition was always preceded by a careful examination of each aphid which might enclose a primary parasite larva. This examination took 10 to 15 minutes. During this time the female *Asaphes* sought an aphid skin which enclosed a late larva or early pupa of the primary parasite *Aphidius testaceipes*. Only an aphid skin which had turned brown after primary parasitization was selected for attack. After moving around such an aphid and palpating its dead body with her antennae, the *Asaphes* mounted it and took a stance with her antennae pointing downward, preliminary to the final act of oviposition. This act took longer and was quite different in its behavioristic pattern than that of the primary parasites. First the female, after squatting slightly, began drilling through the aphid skin with her ovipositor. When the skin was penetrated the ovipositor was slowly pushed in, apparently to locate the primary parasite before the egg was laid. The drilling and egg laying processes required an average of six minutes. Multiple attacks by a single *Asaphes* on one host were not observed, nor attacks by more than one female on the same host.

TABLE 3

Host Stages Selected for Ovipositional Drillings by *Asaphes fletcheri*

Hyper-parasite	*Aphidius testaceipes*		*Praon aguti*	
	Late Larva	Early Pupa	Late Larva	Early Pupa
1	12	20	5	0
2	14	26	9	2
3	0	12	3	1
4	10	13	6	0
5	13	21	8	3
Totals	49	92	33	6

The females of *Asaphes fletcheri* showed a preference for attacking *Aphidius testaceipes* rather than *Praon aguti*. Of the *A. testaceipes* attacked, 65% were in the early pupal stage,

TABLE 4

RATE OF OVIPOSITION BY *Asaphes fletcheri* ON APHIDS ENCLOSING EARLY PUPAE OF *Aphidius testaceipes*

	NUMBER OF OVIPOSITIONS ON SUCCESSIVE DAYS[b]													
Hp[a]	1	2	3	4	5	6	7	8	9	10	11	12	13	TOTAL
1	17	11	0	10	2	2	2	2	0	0	0	1	1	48
2	12	5	8	0	4	3	1	1	1	1	0	0	0	36
3	8	6	6	3	0	0	0	0	0	0	1	0	1	25
4	15	10	6	1	0	0	1	1	1	1	0	0	0	36
5	11	10	0	0	3	1	1	1	0	1	1	0	0	29
6	15	12	0	0	0	0	0	0	0	0	0	0	0	27
Total	78	54	20	14	9	6	5	5	2	3	2	1	2	201

[a]Hyperparasite.
[b]Each hyperparasite given access to primary parasites two hours per day.

35% were late larvae. In the case of *P. aguti* there was even stronger discrimination between the stages, but in the reverse direction, 84% of those attacked being late larvae and only 16% early pupae (Table 3). Details of this selective behavior of the hyperparasite are presented under "Host Relationships" later in this paper.

When females were allowed to oviposit only for two hours per day, their total periods of oviposition ranged from a minimum of two days to a maximum of 13 days. The greatest number of ovipositional drillings took place on the first day. For the next three or four days their number declined rapidly, but they continued at a low level till the thirteenth day (Table 4).

Perhaps the longer period of oviposition in *Asaphes fletcheri*, as compared with that of the primary parasites, results from the longer time required to effect each ovipositon—an act accomplished by the primary parasites in a fraction of a second. If this is true in the field, as well as in the laboratory, many primary parasites are bound to escape the assults of *A. fletcheri*.

ECOLOGICAL RELATIONSHIPS OF *Asaphes fletcheri*

Abundance.—Collections were made in three selected localities on the campus to determine the abundance of *A. fletcheri*, and also of the two primary parasites. Station A was shrubby and open, Station B was shrubby and shady, and Station C was grassy and open, with widely scattered apple trees. Collections were made on three days a week from May to October, 1954, with one hour spent at each station, and with collecting times alternated among them. Each area was swept with a net, and the parasite species in the material collected were identified and counted in the laboratory. The results are given in Table 5.

The total number of *Praon aguti* collected was remarkably uniform at all three stations, but *Aphidius testaceipes* was equally plentiful only at Station C. Only three-fourths as many *A. testaceipes* were taken at Station A, and at Station B this species was hardly more than one-fifth as numerous as *P. aguti*. *Asaphes fletcheri* was most abundant at Station B, and was about 15% less numerous at Station C. Its presence in the last named locality seemed not to affect the population of either primary parasite, perhaps because environmental conditions here limited its attacks on them. Observations made at Station A support this view. At this station *A. fletcheri* was found to be about 16% less numerous than at Station C, but the population of *A. testaceipes* was 24% smaller. The greatest reduction in the population of *A. testaceipes* occurred at Station B, where favorable environmental conditions enabled *Asaphes fletcheri* to play a very destructive role.

TABLE 5

ABUNDANCE OF *Asaphes fletcheri* AND ITS HOSTS *Aphidius testaceipes* AND *Praon aguti* AS SHOWN BY COLLECTIONS MADE FROM MAY TO OCTOBER AT THREE STATIONS

	STATION A	STATION B	STATION C
A. fletcheri:			
May	0	2	2
June	30	10	65
July	31	66	10
August	8	25	7
September	0	1	0
October	4	0	3
Total	73	104	87
A. testaceipes, total	188	52	248
P. aguti, total	245	247	245

The reduction of the population of *A. testaceipes* indicated that in the field *A. fletcheri* preferred that species to *Praon aguti*. Further, the seasonal curve of abundance of *A. fletcheri* was found to follow more closely that of *A. testaceipes* than that of *P. aguti*, which too indicated a preference for the former species. It is also apparent that the hyperparasite was more sensitive than the primary parasites to environmental factors, since

it showed significantly greater destructiveness in one locality only.

Field studies showed that the final reduction in numbers of *Asaphes fletcheri* was due to the absence of suitable hosts for hyperparasitization. At the end of the season it could not be found in these three localities. It still occurred, however, in other neighboring localities at this time.

Longevity.—Under laboratory conditions, when supplied adequate food and numerous suitable hosts, adult females of *A. fletcheri* lived about 24 days. The life span of adult males was a few days shorter. Without food or hosts, females lived an average of 6.2 days, males only half as long.

Effect of Temperature on the Rate of Ovipositional Attempts.—Experiments were conducted at four different temperatures (26°, 28°, 30°, and 32° C.), using the equipment described above. At each temperature ten mated females were individually given access to fresh groups of dead, sessile aphids containing the immature stages of *Aphidius testaceipes*.

At all four temperatures *Asaphes fletcheri* attempted much fewer ovipositions than either of the primary parasites. This may be due to the longer time taken by this species to effect an oviposition, as was stated above. There was much less variation, however, in the number of attempts at the different temperatures than was found in the other species. The maximum number of attempts at oviposition occurred at 28° (Table 6). At 32° the number was only about one-third as large, yet was almost equal to that of either primary parasite at the same temperature. This may be due in part to the fact that the hyperparasite is not handicapped by movements of the primary host as are the

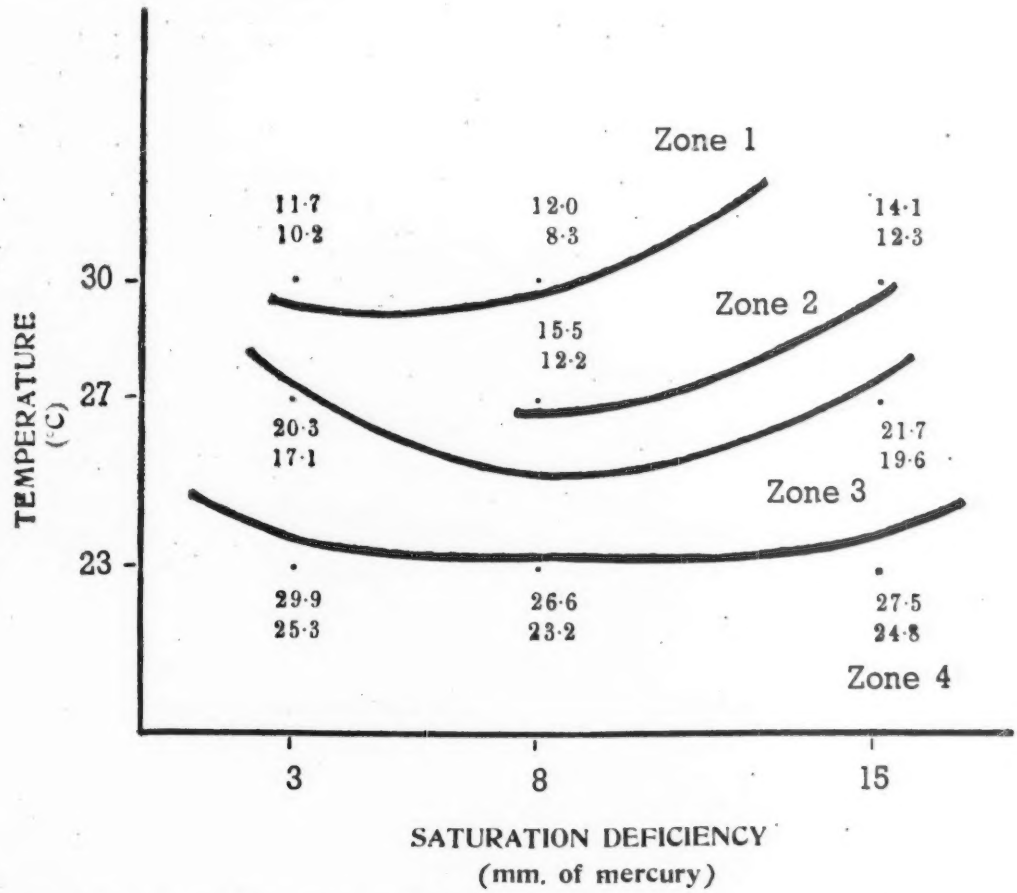

FIG. 1. Effect of temperature and moisture on the length of the life cycle of *Asaphes fletcheri*. Zones delimit approximately equal lengths of life cycles in days. Upper figures refer to females, lower figures to males.

primary parasites. 85% of the ovipositional attempts observed in this experiment resulted in the production of female offspring.

Effects of Temperature and Moisture on Length of Life Cycle.—The length of the life cycle of *Asaphes fletcheri*, from deposition of the egg to emergence of the adult, was determined at temperatures of 23°, 27°, and 30° C., with three saturation deficiencies (3 mm., 8 mm., and 15 mm.) used at each temperature. Twelve of the hyperparasites were reared in each such temperature-moisture combination.

The effect of temperature (Figure 1) is apparent from the fact that the length of the life cycle decreases at higher temperatures. The effect of humidity was much less marked. However, the most rapid development at all temperatures was obtained at the intermediate (8 mm.) saturation deficiency. It was noted also that, under all the experimental conditions tested, the life cycle required a shorter time in males than in females due to the fact that the pupal stage lasted slightly longer in females than in males. The durations of the egg and larval stages were about the same in both sexes.

TABLE 6

NUMBER OF OVIPOSITIONAL ATTACKS MADE BY TEN MATED FEMALES OF *Asaphes fletcheri* AT DIFFERENT TEMPERATURES

°C.	TOTAL NUMBER
26	71
28	95
30	60
32	30

Throughout the experiment the combined duration of the egg and larval stages was found greater than that of the pupal stage, whereas the reverse was true in the case of the primary parasites. Thus, at 27° C. and a saturation deficiency of 15 mm. (approximately 47.5% relative humidity), the egg and larval stages took 11.2 days in the males and 11.9 days in the females, which was more than double the time required by the primary parasites.

Host Relationships.—Like the primary parasites, the hyperparasites have certain general requirements which must be fulfilled by their various host species. Just as there are many factors checking the undue increase of primary parasites, so also are there factors preventing excessive increase in the numbers of hyperparasites. Muesebeck and Dohanian (1927) have given an account of these factors, which were found generally applicable to *Asaphes fletcheri*. Careful observations did not reveal any tendency among the several adult hyperparasites toward feeding on the hosts.

Host Selection.—Hyperparasites generally are less discriminating than primary parasites as regards selection of hosts, according to Muesebeck and Dohanian (1927). While this concept may be largely true, there are exceptions to the rule. Certainly *Asaphes fletcheri* exhibited a marked degree of discrimination in selecting its host species. Spencer (1926) and Griswold (1929) had established that this species would attack only dead, sessile aphids. This was confirmed by the present writer.

Two other phenomena came to light which demonstrate the existence of a high degree of discrimination in *A. fletcheri*. The first one, also noted by Spencer (1926), was that the hyperparasite only attacked late larval or early pupal stages of *Aphidius testaceipes*. The present studies not only supported this, but also revealed the second fact, namely, that *A. fletcheri* definitely preferred the early pupal stage of *A. testaceipes* and the late larval stages of *Praon aguti*. These conclusions are based on the following experiments.

Five *Asaphes fletcheri* were studied individually with a population of each of the primary parasites. In the first experiment 50 dead, sessile aphids containing *Aphidius testaceipes*, and 50 containing *Praon aguti*, were used. Half the primary parasites of each species were in the late larval stage, half in the pupal stage, and these stages were exposed simultaneously to hyperparasitization. Each hyperparasite was allowed to attack two hours each day for five days. In the second experiment again both primary parasites were used, but their larval and pupal stages were exposed separately to attacks of *Asaphes fletcheri*, one hour each day for five days.

TABLE 7

AVERAGE NUMBERS OF OVIPOSITIONAL ATTEMPTS PER FEMALE *Asaphes fletcheri* WHEN (1) TWO IMMATURE STAGES (25 INDIVIDUALS EACH) OF EACH HOST WERE EXPOSED TOGETHER TO ATTACK FOR TWO HOURS, AND (2) WHEN 25 INDIVIDUALS OF EACH STAGE WERE EXPOSED SEPARATELY FOR ONE HOUR

	Aphidius testaceipes		*Praon aguti*	
	LATE LARVA	EARLY PUPA	LATE LARVA	EARLY PUPA
(1)	8 9	22 3	5 3	1 2
(2)	10 3	24 2	7 3	0

When the two stages of *Aphidius testaceipes* occurred together, 89.2% of the aphids enclosing early pupae were attacked, as compared with 35.6% of those containing late larvae. With *P. aguti* the preference was reversed, 21.2% of the aphids with late larvae and only 4.8% of those with pupae being attacked. When the two stages of *A. testaceipes* were exposed separately, 96.8% of the early pupae, 41.2% of the late larvae were attacked. Thus *Asaphes fletcheri* showed a definite preference for the early pupal

stage of *Aphidius testaceipes*. When these two stages of *Praon aguti* were exposed separately none of the pupae were attacked, and the number of attacks on late larval stages was slightly higher than occurred on the same stage when the two stages were exposed together. Thus with *Praon aguti* it was the late larval stage rather than the pupa which was preferred.

The second phenomenon indicating a high degree of discriminative ability was that *Asaphes fletcheri* attacked a much higher percentage of the available *Aphidius testaceipes* than of the available *Praon aguti* (Table 7). These experiments confirm the field observations as regards the preferential selection of the former over the latter primary parasite.

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OBSERVATIONS ON EGYPTIAN HYALOMMA TICKS (IXODOIDEA, IXODIDAE). I. PARASITISM OF LIZARDS BY NYMPHS[1]

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INTRODUCTION

Various species in the genus *Hyalomma* are the ticks most commonly encountered from Northwest Africa to India. Only a single other tick, *Rhipicephalus sanguineus* (Latreille), closely challenges this assertion. Hyalommas have been associated with a greater number and variety of pathogenic organisms than any other group of ectoparasites. Nonetheless their taxonomy has long been chaotic and the biology of most species remains poorly understood. Biological concepts in this genus, based largely on veterinarians' research in farmyards and heavily grazed areas, derive from observations by several Soviet and a few French workers, the latter chiefly studying *H. detritum* (= *H. mauritanicum*) in Algeria. Valuable as these observations are in the absence of more extensive studies, they have resulted in obvious misconceptions concerning the biology and life cycle of *Hyalomma* ticks away from large concentrations of domestic animals. Even where numbers of domestic animals are involved, the rôle of smaller wild vertebrates in the maintenance of hyalommas must not be overlooked. Evidence suggests that the life cycles of several species in this genus vary as a result of the presence or absence of smaller animals that may serve as hosts of the parasite's immature stages (Hoogstraal 1956a, pp. 442–4).

The object of the present series of reports is to provide biological data on Egyptian species that will indicate the relationships of *Hyalomma* ticks not only to domestic animals but to the entire fauna of this area, and also to bolster taxonomic criteria in this genus.

MATERIALS AND METHODS

Hosts were collected incidental to a survey of Egyptian vertebrate and ectoparasite fauna (Hoogstraal 1955, 1956b). Since much travelling and several diversified research projects were

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[2]With the technical assistance of Sobhy Gaber.

undertaken concurrently, only a few of the small vertebrates found infested by ticks in nature could be held alive in the laboratory for further observation. Whenever time and facilities permitted, tick-infested hosts were placed with food and water in a glass battery jar covered by a tightly fitting wire-screen of quarter inch mesh. Some hosts, such as lizards, were fed living mealworms by hand. The jar, inverted over a hole of slightly less than its own diameter, was enclosed at the wire-screened end by a twelve-inch long muslin bag held tightly against the glass sides by means of an elastic seam. The bag was replaced each day and engorged ticks that had fallen from the host and through the wire mesh were sorted from the fecal pellets and food particles that had also fallen into the bag. This procedure was repeated until all ticks had left the host. Engorged ticks were stored in individual plastic tubes, one end of which was closed by plaster of Paris and the other by muslin, placed in moist sand (after Kohls 1937), and maintained at room temperature until they molted to nymphs or adults, a few days after which they were preserved in 70% alcohol. Cast skins were given the same catalog number as the individual adult tick. These exuviae are presently being mounted for further comparative morphological study. Nymphs reared to adults in the manner described above are referred to as "reared nymphs" in this series of reports.

A small number of individuals that fell as engorged larvae were reared to the adult stage, and some adults were kept alive for study of their life cycle and progeny. Time and facilities restricted this phase of investigation which is now commencing on a larger scale.

During extended field trips throughout Egypt, many quite fully engorged nymphs were found on animals which were obtained by shooting or trapping and immediately prepared as study specimens. Nymphs removed from these hosts were frequently placed alive in tubes and returned to the laboratory for observation. Although mortality among such nymphs was high, certain valuable data were obtained and these are included in the present series of reports.

NYMPHS FROM LIZARDS

During 1955 and 1956, 79 lizards, *Acanthodactylus boskianus asper* (Audouin), were found infested by larval and nymphal *Hyalomma* ticks in Giza Province near Cairo. The localities were Giza Pyramids, Giza, Kirdasa, Abu Rawash, and El Mansuriya.

Seventy-two of the above hosts were infested by either 1 or 2 nymphs. Seven hosts, infested by 3, 4, 5, 7, 8, 9, and 12 nymphs respectively, were collected from May through October.

Fifteen of the above hosts yielded 40 *Hyalomma* nymphs that died before molting and cannot yet be identified. Three of these hosts also yielded larvae that molted to nymphs but have not been identified.

Fifty-nine lizards collected in the months noted below yielded 87 nymphs that molted to adults as indicated in Table I. Two of the hosts were infested by nymphs of both *H. impeltatum* and *H.* sp. no. 1 near *excavatum*. Two additional hosts, not included in the tabulation, yielded nymphs that molted to dwarf adults provisionally identified as *H. excavatum*. Nymphs and larvae were found chiefly in the host's axillae, also on the neck and flanks, during all months of the year.

TABLE I

MONTH BY MONTH COLLECTION OF LIZARDS THAT YIELDED NYMPHAL TICKS

TICK SPECIES	HOSTS COLLECTED (BY MONTH)													
	♂♂	♀♀	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
H. impeltatum	9	17	0	0	0	1	0	2	8	3	1	2	1	1
H. sp. no. 1 near *excavatum*	35	25	1	5	2	2	9	1	0	1	11	5	1	3
H. dromedarii		1	0	0	0	0	0	0	0	1	0	0	0	0
Total	44	43	1	5	2	3	9	3	8	5	12	7	2	4

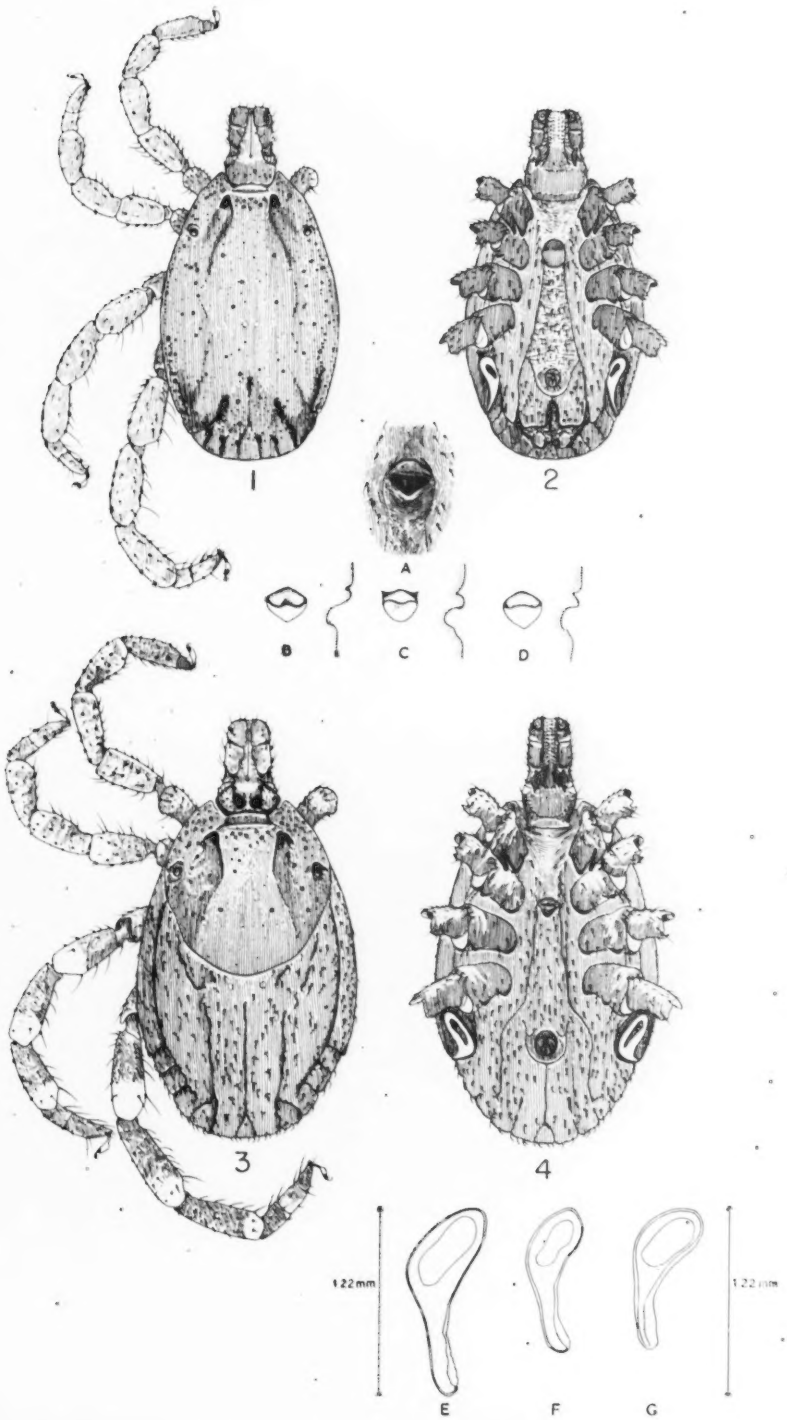
The data for month of collection of host are insufficient definitely to determine a seasonal cycle in nature. *Acanthodactylus boskianus asper* is a common desert-edge lizard of Lower Egypt.

In both tick species, the time between dropping

EXPLANATION OF FIGURES

FIGS. 1–4.—*Hyalomma* species no. 1 near *excavatum*. FIG. 1. Male, dorsal view. FIG. 2. Male, ventral view. FIG. 3. Female, dorsal view. FIG. 4. Female, ventral view.

Insets: A, female genital area. B to D, genital area, outline and profile, unengorged and unmated. E to G, spiacular plates of, respectively, *Hyalomma* species no. 2 near *excavatum*, *H. excavatum*, and *H.* species no. 1 near *excavatum*.


1
2
A
B
C
D
3
4
1.22 mm
1.22 mm
E
F
G

from the host and molting to the adult stage varied considerably with season. Nymphs that dropped from December through March required mostly from 67 to 83 days before molting. In April this interval was reduced to 40 days, and afterwards till mid-October to from 21 to 26 days. After mid-October, the length of this period again increased. Nymphs were held at unheated room temperature.

Numerous additional records of unidentified *Hyalomma* larvae and nymphs from other *Agama* and *Acanthodactylus* lizards in the Cairo area are listed in our data books.

OBSERVATIONS ON *H.* SP. NO. 1 NEAR *excavatum*

"Although probably already described, we are not yet certain which name applies to this species" (Hoogstraal 1956a, p. 881). As noted above, nymphs parasitize *Acanthodactylus* lizards throughout the year in the vicinity of Cairo. As indicated in Table I, this is the most frequent immature tick found on Egyptian lizards.

Miscellaneous rearings: Five adults of *H.* sp. no. 1 near *excavatum* were reared from nymphs from four lizards and one spiny mouse (*Acomys*) with the following data:

1 ♀ *ex* "Lizard", collected April 1951, at Abu Rawash (near Cairo).
1 ♂ *ex Acanthodactylus boskianus asper*, collected 24 May 1953 at El Amiriya (near Alexandria).
1 ♀ *ex Agama mutabilis* Merrem, collected 16 June 1953 on the littoral desert at El Amiriya (near Alexandria).
1 ♂ *ex Acanthodactylus s. scutellatus* (Audouin), collected 26 March 1951 on the littoral desert at El Alamein (Western Desert). This specimen was determined as *H. excavatum* by Dr. L. P. Delpy in December, 1952.
1 ♀ *ex Acomys russatus* (Wagner, 1840), collected 16 November 1952 at St. Catherine's Monastery, 5000 feet elevation (southern Sinai).

Adult collections: A male of *H.* sp. no. 1 near *excavatum* was taken from a land tortoise at Gheminez, Cyrenaica, Libya, on 30 October 1955 by Sayed Mitwally of the NAMRU3 Medical Zoology staff. A female of the same species was taken from a camel at Siwa Oasis, Egypt, on 28 March 1951 by H. Hoogstraal. The latter specimen was identified by Dr. Feldman-Muhsam as *H. truncatum*, a species known in Egypt only from the far southeastern corner (Hoogstraal and Kaiser 1957).

Life cycle: The results obtained from rearing the progeny of a single pair of *H.* sp. no. 1 near *excavatum* that had molted to adults on 21 June (♂) and 27 June (♀) from nymphs from *Acanthodactylus boskianus asper* taken at Kirdasa, Imbaba, Giza, on 30 May 1955 (rearing lot 104) are shown in Table II.

Nonfeeding individuals were maintained at room temperature. Hosts of adults were laboratory rabbits; lizards served as immature-stage hosts.

Two other pairs of adults fed fully on the arm of a human volunteer for four days. Intense itching at the sites of insertion was felt after the second day and, less severely, for several weeks after detachment.

DISCUSSION

Undoubtedly, once the very definite characteristics of *H.* sp. no. 1 near *excavatum* are generally recognized (figs. 1 to 4) additional specimens will be revealed and more extensive biological and distributional data will be added to the meagre store of available information concerning this species, which quite likely has a prior name.

TABLE II

LIFE HISTORY DATA ON THE PROGENY OF A PAIR OF *H.* SP. NO. 1 NEAR *excavatum*

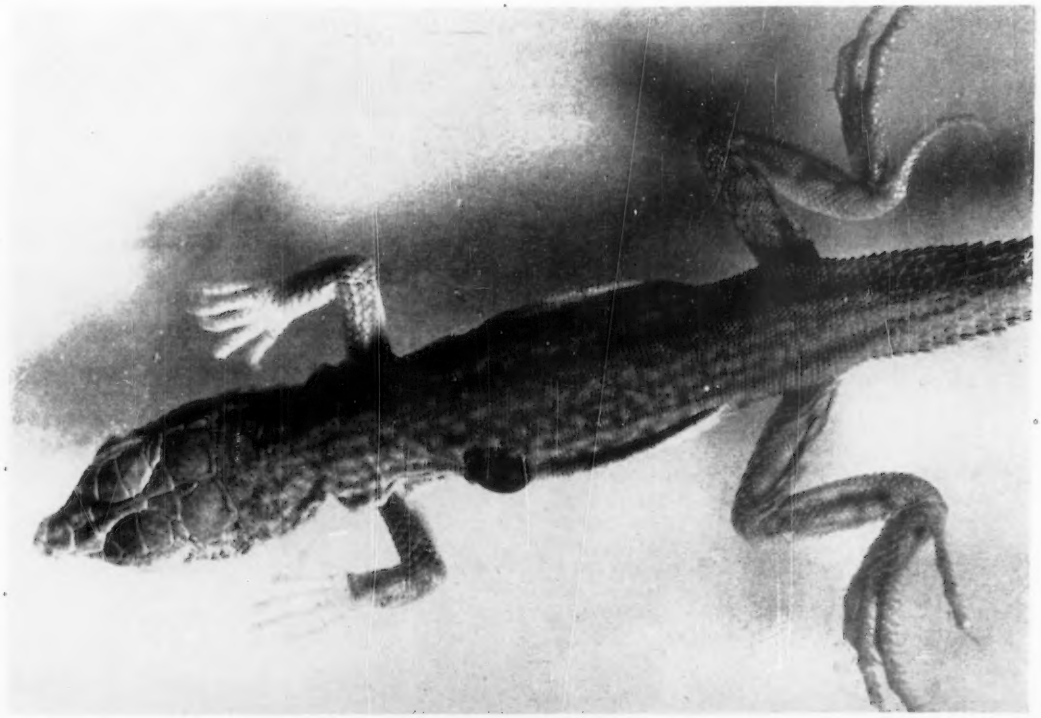
DATE	EVENT	DAYS
18 July 1955	adults commenced feeding	
23 July	♀ detached from host	6
4 Aug	oviposition commenced	12
20 Aug	larvae hatched	28
26 Sept	larvae commenced feeding	29
28 Sept to 10 Oct	larvae detached	2 to 14 (av. 8.3)
13 Oct to 24 Oct	nymphal molt	11 to 16 (av. 15.0)
18 Oct to 15 Nov	nymphs commenced feeding	2 to 21 (av. 4.3)
7 Nov to 5 Dec	nymphs detached	15 to 27 (av. 20.0)
20 Dec to 28 Feb	adult molt	30 to 108 (av. 52.0)

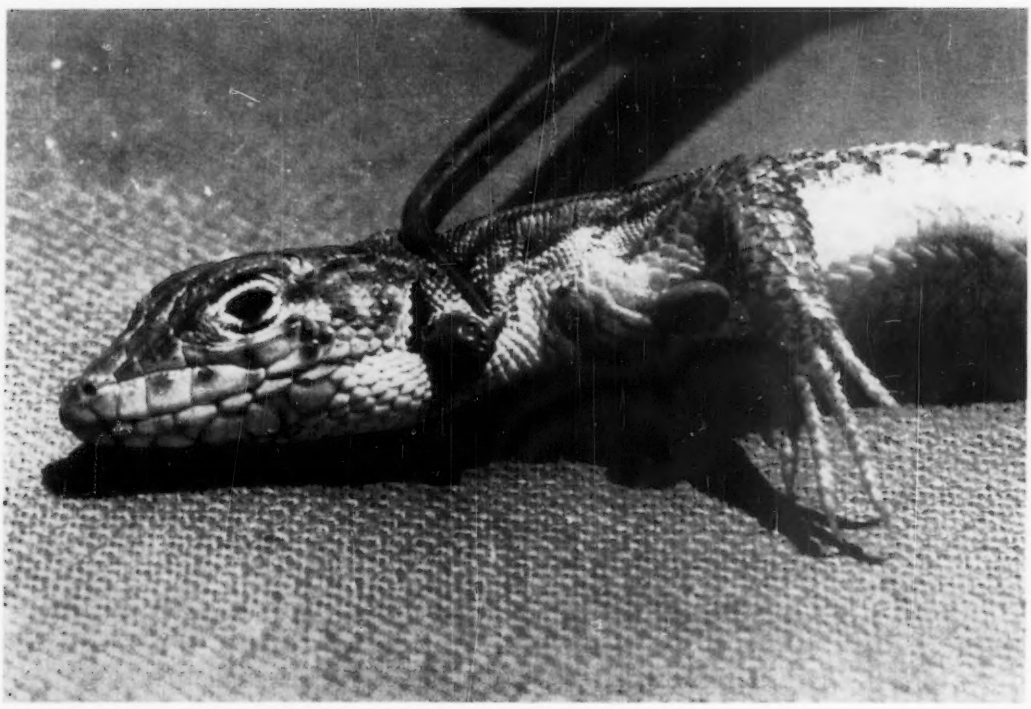
Total: Oviposition to F1 adults: Min. 117, Max. 240, Av. 153.7 Days.

The presently known geographical range of this species extends from the mountains of southern Sinai to Cyrenaica in Libya. Although immature stage hosts of predilection are lizards of the littoral desert (El Amiriya and El Alamein) and desert edge (Giza Province), spiny mice, *Acomys*, are also infested in arid Sinai mountains. The rarity of wild-caught adults in our collections intimates a specialized host preference that remains to be determined. Finding of an adult on a Libyan land tortoise suggests that where these cold-blooded vertebrates are present, they may be acceptable or preferred hosts. However, tortoises have become extinct in Egypt within recent times, except near the Libyan and Palestinian frontiers, and only *H. aegyptium* has been recovered from tortoises near Palestine. No ticks were found on a number of land tortoises examined in Egypt near the Libyan frontier.

EXPLANATION OF FIGURES

FIG. 5.—*Acanthodactylus* lizards infested by nymphs of *Hyalomma impeltatum* and *H.* species no. 1 near *excavatum*. Egypt





Further biological study of this tick in Libya might be especially interesting.

SUMMARY

Seventy-nine specimens of the lizard *Acanthodactylus boskianus asper* (Audouin), collected during all months of 1955 and 1956 on the desert edge near Cairo, were infested by immature *Hyalomma* ticks. Nymphs from 59 of these lizards were reared to 9 males and 17 females of *Hyalomma impeltatum*, 35 males and 25 females of *H.* sp. no. 1 near *excavatum*, and a single male *H. dromedarii*. Other nymphs were reared to unidentifiable dwarf adults, and other non-reared and unidentified *Hyalomma* nymphs and larvae were also found on the above lizards. Engorged nymphs of the first two tick species noted above molted to adults in from 21 to 26 days in summer and from 67 to 83 days in winter.

H. sp. no. 1 near *excavatum* nymphs reared to adults were also secured from the same form of lizard on the Mediterranean littoral of the Western Desert; from other lizards, *Acanthodactylus s. scutellatus* and *Agama mutabilis*, in the same area; and from a spiny mouse, *Acomys russatus*, in the mountains of southern Sinai. Adults have been found infesting a camel in an Egyptian oasis and a land tortoise in Libya. The known geographical range of this species extends from the mountains of Sinai through the deserts of Egypt into Cyrenaica, Libya. In the laboratory, the life cycle from oviposition to F_1 adults required 117 to 240 days, average 153.7 days. Lizards were utilized as experimental hosts for immature stages and rabbits for adults. Adults also engorged on man.

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OBSERVATIONS ON EGYPTIAN HYALOMMA TICKS (IXODOIDEA, IXODIDAE).

2. PARASITISM OF MIGRATING BIRDS BY IMMATURE H. RUFIPES KOCH[1]

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INTRODUCTION

Data from tick-infested birds passing the Cairo area en route to Europe and Asia lucidly illustrate potentialities for introduction and establishment of isolated tick populations far from the parasite's native range in the Ethiopian Faunal Region. The birds recorded below were trapped in the environs of Cairo on their northward, spring migration. The summer and winter range and migratory habits of each form, briefly abstracted from Meinertzhagen (1930), are included in the present report in order to show the time and geographical area into which their African tick parasites may be introduced. Miscellaneous records from a few other local tick-infested birds are appended for comparative purposes. Methods have been described by Hoogstraal and Kaiser (1957).

RECORDS FROM SPRING MIGRANTS

Oenanthe o. oenanthe (Linnaeus). European Wheatear

The European Wheatear breeds throughout most of Europe, east to central and northern Asia and northern Alaska, also in Corsica and northern Palestine but not in Cyprus or Crete. It migrates to Arabia, Africa south to the Zambesi River, and India. Many Asiatic birds probably winter in Africa or Arabia. It is abundant in Egypt and Sinai on both passages, first arriving in the latter half of August and disappearing by mid-November. Spring passage, commencing in early March, is completed late in May. A bird

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[2]With the technical assistance of Sobhy Gaber.

of open country, it is usually found on fringe of cultivation and desert.

Thirty-two European Wheatears infested by nymphal hyalommas were trapped in March and April 1956. Engorged nymphs dropped from the birds two to four days after capture; others were removed when the host died. Fifty-nine nymphs molted to 20 males and 39 females of *H. rufipes* between 1 and 23 May, 4 to 6 weeks after dropping or detachment from the host. In addition, 66 larvae and 46 nymphs, probably mostly *H. rufipes*, from these birds died before molting. Mortality of immature ticks from heavily infested birds was high. Eleven hosts yielded the 112 immature specimens that died; among them 5 were infested by from 6 to 58 larvae and nymphs. The other 27 hosts, infested by fewer than 6 and mostly by 1 or 2 ticks, provided vigorous specimens that were reared with few deaths.

Oenanthe isabellina (Cretzschmar). Isabelline Wheatear

This bird breeds in southeastern Russia, Asia Minor, Syria, possibly in extreme southern Palestine and northern Sinai, eastern Turkestan, Beluchistan, Tibet, and Mongolia. It winters in northern India, Arabia, Egypt, Sinai, the Sudan, and East Africa as far as Tanganyika. It is common in Egypt and Sinai during southward passage from August to October; it is fairly common in winter but apparently does not breed in Egypt; it returns northward between mid-March and early May.

Nineteen Isabelline Wheatears bearing 185 nymphal hyalommas were trapped in March and April 1956. These nymphs molted to 54 males and 57 females of *H. rufipes* and 2 females of *H. impeltatum* between 26 April and 21 May. One host was infested by both species of ticks, which do not generally inhabit the same ecological areas. An additional 22 larvae and 50 nymphs that died before molting were obtained; these were probably mostly *H. rufipes*. Fourteen hosts were infested by only 1 or 2 nymphs. Host number 353 yielded 103 nymphs, 25 of which died and 78 of which molted to 41 males and 37 females of *H. rufipes*. Four other birds were infested by 3, 5, 12, and 26 immature ticks respectively. All nymphs that molted became adults between 26 April and 21 May. The interval between dropping or being removed from the host and molting to the adult stage varied from 1 to 2 months with 6 weeks being the usual length of time. However, those on the single heavily-infested bird, mentioned above, all molted exactly 1 month after being removed from the host.

Oenanthe hispanica melanoleuca (Güldenstadt). Black-Eared Wheatear (Eastern Form)

This bird breeds in Crimea, Bulgaria, Balkan Peninsula, Asia Minor, Palestine, western Iran, Crete, and Aegean Islands, but apparently not in Cyprus. It straggles to southern Sahara and northwestern Africa, British Isles, and Malta. It winters through Egypt, Sinai, Sudan, Ethiopia, and Red Sea coast. In Egypt and Sinai it is more abundant in spring than in autumn; autumn passage extends from early September through first week of October; spring passage extends from early March through late April. A few probably winter in Upper Egypt.

Eleven hosts collected in last week of March and first half of April, 1955 and 1956, yielded 16 nymphs that molted to 9 males and 7 females of *H. rufipes*, plus 65 larvae and 35 nymphs probably of this species. All nymphs molted to adults between 9 and 21 May.

Phoenicurus p. phoenicurus (Linnaeus). Common Redstart (Western Form)

This bird breeds throughout most of Europe; it migrates into Arabia and Africa but apparently does not reach the equator. It arrives in Egypt early in September and October, passes northward between 15 March and 10 May; it is abundant during both passages, but absent in winter.

Five hosts trapped between 23 March and 13 April 1956 yielded 6 nymphs that molted to 4 males and 2 females of *H. rufipes* on 12 and 21 May.

Erythropygia g. galactotes (Temminck). Rufous Warbler

This bird is distributed from southern Spain and Portugal through littoral northern Africa to Palestine and southern Syria, also into northern Sudan; it winters in Sudan and southern Sahara. It is a summer visitor in Egypt along the Mediterranean littoral, in the Nile Delta, Upper Egypt and the Egyptian oases; also in northern Sinai. Earliest Egyptian arrivals were noted 12 March, but it became more numerous during first week of April and departed in September.

Three birds trapped on 9, 10, and 12 April 1956, nymphs removed day following capture; one host yielded 3 nymphs, probably *H. rufipes*, that died; the second yielded a single nymph that molted to a female *H. rufipes* on 17 May, and the third, 10 nymphs that molted to 3 males and 7 females of *H. rufipes* also on 17 May.

Monticola saxatilis (Linnaeus). Rock Thrush

This bird breeds in isolated mountains of Europe, southern Russia, Asia Minor, Lebanon, Iran, Beluchistan to southern China, also in Morocco and Algeria. It is nowhere common. A strong migrant, it winters almost entirely in Africa—a remarkable example of winter concentration from a wide breeding area. Spring passage in Egypt is very marked from end of March to first half of April; autumn passage is less marked.

Two Rock Thrushes were trapped on 20 March

and 1 April 1956. Nymphs pulled on 22 March and 2 April respectively all molted to adult *H. rufipes* on 12 May. A single female was reared from the first host and 1 male and 5 females from the second host.

Anthus c. campestris (Linnaeus). Tawny Pipit

This bird is distributed through practically the whole of Europe to western Asia. It winters throughout Africa north of the equator. It is abundant on spring and autumn passage in Egypt and Sinai.

Two nymphs, removed on 12 and 13 April 1956 from two Tawny Pipits that had been trapped a few days earlier, molted to males of *H. rufipes* on 16 May.

Calandrella b. brachydactyla (Leisler). Short-Toed Lark (Mediterranean Form)

This bird is distributed from southern Europe, North Africa and Crete to Asia Minor. It passes through Egypt and Sinai in large numbers in spring, through the first week of April, and in autumn beginning late in August; a few remain in Egypt during the winter.

Two nymphs, removed on 9 April 1956 from a Short-toed Lark trapped the day previously, molted to 2 females of *H. rufipes* on 12 May.

Lanius nubicus Licht. Masked Shrike

This bird breeds from Asia Minor to southwestern Iran (also, formerly in Greece). It winters in Iraq, Arabia, and the Sudan; it has not been recorded south of Lake Rudolph. In Egypt, it is more abundant on spring passage, 12 March to 25 April, than on autumn passage. A few winter in Upper Egypt and near Wadi Halfa in the Sudan.

A nymph moved from a Masked Shrike on 21 March 1956 molted to a male *H. rufipes* on 23 May.

Lanius s. senator Linnaeus. Woodchat (European Form)

This bird is distributed in Europe north to Belgium, Holland, and Germany; east to southern Russia and the Caucasus. It winters in Africa north of the equator. It is abundant in Egypt on spring passage, 16 March to 22 April, but rare in autumn; it is not present in winter.

A Woodchat trapped 11 March 1956 died 2 days later; the nymph removed from it on that date molted to a female *H. rufipes* on 12 May.

RECORD FROM FALL MIGRANT

Coracias g. garrulus Linnaeus. Roller (Western Form).

This bird breeds in northwestern Africa, throughout most of continental Europe to the Caucasus, Cyprus, and Palestine, but apparently not in Crete. It winters to South Africa. It is common in Egypt on autumn passage, arriving first on 30 July, mostly between the end of August and mid-September; the latest record is 30 September. It is rare on spring passage; it seldom appears before 26 April (very late for a spring migrant in Egypt); the latest record is 18 May. Adults arrive first in Egypt in autumn; they migrate in parties of 3 to 10 or more and cross the sea at about 1000 feet elevation in fine weather.

An immature Roller trapped at Abu Rawash on 10 September 1956 was infested by a single nymph that detached on 14 September and molted to a male *H. marginatum* on 27 September. Populations of *H. marginatum* are exceedingly small, scarce, and localized in Egypt and the Sudan.

MISCELLANEOUS RECORDS

The following miscellaneous records provide additional insight into parasitism of Egyptian

TABLE 1

SUMMARY OF *Hyalomma* TICKS COLLECTED AND REARED FROM MIGRANT SPRING BIRDS NEAR CAIRO

Host	Number of Hosts	*H. rufipes* Nymphs Reared to Adults		Unidentified Larvae & Nymphs		Total Ticks
		♂♂	♀♀	L	N	
Oenanthe o. oenanthe	32	20	39	66	46	171
Oenanthe isabellina[a]	19	54	57	22	50	183
O. h. melanoleuca	11	9	7	66	35	117
P. p. phoenicurus	5	4	2	0	0	6
Erythropygia g. galactotes	3	3	8	0	3	14
Monticola saxatilis	2	1	6	0	0	7
Anthus c. campestris	2	2	0	0	0	2
Calandrella b. brachydactyla	1	0	2	0	0	2
Laninus nubicus	1	1	0	0	0	1
Lanius s. senator	1	0	1	0	0	1
Total	77	94	122	154	134	504

[a]One of these hosts also yielded two nymphs that molted to females of *H. impeltatum*

birds, stress the need for development of criteria for identifying immature hyalommas, and demonstrate the impossibility of conclusions concerning origin of infestation when the host is so worn that it cannot properly be identified to subspecies by a qualified ornithologist.

Falco tinnunculus SSPP. Kestrel

It has been impossible satisfactorily to differentiate to subspecies the study skins of four worn, tick-infested Kestrels trapped at Abu Rawash near Cairo. The European form (subspecies *tinnunculus* Linnaeus) migrates to Egypt while the local form (subspecies *rupicolaeformis* Brehm) occurs throughout Egypt east of Alexandria, Sinai, southwestern Arabia, northern Sudan and northern Somaliland. Nymphs from three birds taken in March 1956 yielded 2 males and 1 female of *H. rufipes*, 1 dead *Hyalomma* nymph, and 1 female *R. s. sanguineus*. Another Kestrel trapped at the same locality on 4 September 1956 dropped 3 nymphs 4 days later that molted on 2 October to 2 males and 1 female of *H. rufipes*.

The first three of these birds may have been local or northward migrants, the fourth was either local or a southward migrant. The rarity of *H. rufipes* populations in the Cairo area suggests that these infestations may have been obtained elsewhere.

Lanius minor Gmelin. Lesser Gray Shrike

Two larvae and 1 unidentified *Hyalomma* nymph were obtained from a Lesser Gray Shrike at Kom El Hanash, Abu El Matamir, Beheira (saline area on the edge of the Nile Delta and the Western Desert), on 24 February 1953 by H. Hoogstraal. This bird is an inhabitant of Europe and Asia that winters in tropical and southern Africa. It is stated to be very rare on the spring passage in Egypt, and its occurrence here late in February, as well as the extensive area in which it winters and from which it may have acquired these ticks is of interest.

Aethene noctua saharae (Kleinschmidt). Little Owl (Saharan Form)

A single unidentifiable *Hyalomma* nymph was taken from a Little Owl at Burg El Arab, some 30 miles west of Alexandria in the Western Desert, on 27 January 1954, by M. N. Kaiser. This is a resident bird on the Mediterranean littoral from Syria to Morocco. *Hyalomma* species known to occur in the vicinity of Burg El Arab are *H. dromedarii*, *H. excavatum*, *H. impeltatum*, and *H.* spp. nos. 1 and 2 near *excavatum* of Hoogstraal (1956).

Unidentified Hosts

A single *Hyalomma* larva was taken from *Oenanthe* sp. at Abu Rawash, Imbaba, Giza (near Cairo) on 1 April 1954, by Sobhy Gaber.

The following unidentified *Hyalomma* larvae and nymphs were secured from birds at or near Feiran Oasis, Sinai, 1500 feet altitude, in November 1952, by H. Hoogstraal:

2 "Passerine birds", 10 larvae, and 5 nymphs
Wagtail, *Motacilla* sp., 1 nymph
Sand Grouse, *Pterocles* sp., 2 larvae, and 4 nymphs

DISCUSSION AND CONCLUSIONS

Spring migrants: The ten forms of springtime migrants recorded as hosts are restricted to those easily taken in traps baited with scarab beetle larvae in the environs of Cairo. Some 290 forms of European-Asiatic birds include Egypt in their flyways to and from Africa. Among these, some bypass the Cairo area or rarely linger here and others are not attracted to this bait.

Five hundred and four immature *Hyalomma* ticks were secured from 77 passerine birds, representing 10 forms, passing Cairo during the spring enroute to Europe and Asia. Two hundred and twenty adults of *H. rufipes* were reared from nymphs from these birds and 284 larvae and nymphs, probably most of them *H. rufipes*, died before molting. These data contribute to the conclusion that populations of *H. rufipes* outside of the Ethiopian Faunal Region result largely or entirely from introduction by migrating birds (Hoogstraal 1956, p. 482).

The source of these infestations is eastern Africa, the winter range of the European Wheatear, Common Redstart, and Woodchat. The first of these three flies as far south as the Zambesi River, the other two apparently do not cross the equator. Other migrants, such as the Isabelline Wheatear, Black-eared Wheatear, Short-toed Lark, and Masked Shrike, winter in eastern Africa north of the equator (except the first, which reaches Tanganyika) as well as in Upper Egypt and in a few instances in Lower Egypt. However, the rarity of *H. rufipes* in Lower Egypt suggests that the ticks were acquired from the larger populations further south.

The single pair of *H. impeltatum* reared from these spring migrants probably attached in Upper Egypt, northern Sudan, or northeastern Kenya since this tick is rare and localized in more humid zones of Africa.

The destinations of these tick-infested birds include much of Europe, the Near East, Russia, and southeastern Asia. Many parasites probably remain attached until their hosts reach Europe or Asia for in Cairo, on their way north, few nymphs are fully engorged. Although nymphs feed for 7 to 10 days in the laboratory there is reason to suspect that a certain proportion of nymphs remain attached for longer periods in nature.

Some nymphs undoubtedly detach in Lower Egypt, but infestations of domestic animals by adult *H. rufipes* in the northern Nile Valley and Delta are uncommon and localized. Inclement

ecological factors probably preclude the development of large populations from these potential foci. The statement that *H. rufipes* is common on Egyptian domestic animals in the Nile Valley (Hoogstraal 1956, p. 482) should be qualified by the addition of "in Upper Egypt".

Outside of the Ethiopian Faunal Region, rare, small, sporadic populations of *H. rufipes* occur in Egypt, Libya, Palestine, Anatolia and southern Russia. It is probable, as suggested by Pomerantzev (1950), that these result from introductions by migratory birds. *H. rufipes* is fairly common in the Yemen, but this Kingdom in Southwestern Arabia is a natural extension of the Ethiopian Faunal Region and migrating birds may or may not be an important factor here. Iraq should be deleted from the known range of *H. rufipes*.

Where only one or two immature hyalommas infest a passerine host, the parasites generally have a better chance of surviving than when larger numbers feed on one bird. A single and notable exception, however, was noted in the instance of an Isabelline Wheatear infested by 103 nymphs, 78 of which molted to adults.

All nymphs molted to adults between 26 April and 21 May, mostly in May, whether they were taken in March or April. The average interval between leaving the host and molting gradually decreased, week by week, from March through April.

Further research on the length of nymphal feeding on passerine birds and on the rate of infestation of migrant birds newly arrived at their final destination should be of interest.

Immature *Hyalomma* ticks invariably, in our experience, attach to the bird's head, on the crown, beside the beak, in and around the ears, or beside the eyes.

Autumn migrants: The single autumn migrant trapped during the period of this study, an immature Roller probably from Europe, bore with it a nymphal *H. marginatum*. It appears probable that quite a number of immature *H. marginatum* are introduced into Africa each year on migrating birds of one kind or another. These may account for the small, rare, localized populations of this tick in Egypt and the Sudan and the single male *H. marginatum* known from Kenya, where it was found on a cow after dipping.

ACKNOWLEDGMENTS

We are grateful to Dr. M. A. Traylor, Assistant Curator of Birds at Chicago Natural History Museum for promptly identifying the hosts recorded above, and to Dr. Traylor and Dr. A. L. Rand, Chief Curator of Zoology of the same institution, for kindly reviewing the manuscript and providing comments. G. M. Kohls and Dr. C. B. Philip of the Rocky Mountain Laboratory have also earned our thanks for their review and comments on the manuscript. Study skins of the hosts were prepared by Sayed Mitwally of the NAMRU3 Medical Zoology staff.

SUMMARY

Five hundred and four immature *Hyalomma* ticks were secured from 77 passerine birds, representing 10 forms, passing Cairo during their spring migration en route to Europe and Asia. Two hundred and twenty adults of *H. rufipes* were reared from nymphs from these birds and 284 larvae and nymphs, probably mostly *H. rufipes*, died before molting. In addition, 2 females of *H. impeltatum* were reared from nymphs from one of these birds. All nymphs molted to adults during the last week of April or the first three weeks of May. Most hosts were infested by fewer than 5 nymphs and these survived more frequently than those from heavily infested birds; however, of 103 nymphs from a single Wheatear (*Oenanthe isabellina*), 78 adults were reared. These data support conclusions that *H. rufipes* populations outside of the Ethiopian Faunal Region (Egypt, Libya, Palestine, Anatolia, and southern Russia) have been established from introductions by migratory birds. Records of other *Hyalomma*-infested Egyptian birds are provided for comparative purposes.

A single autumn migrant, a Roller passing Cairo from Europe or Russia en route to tropical Africa, was infested by a nymph that molted to a male *H. marginatum*, a tick rarely found in northeastern or eastern Africa.

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OBSERVATIONS ON EGYPTIAN HYALOMMA TICKS (IXODOIDEA, IXODIDAE).

3. INFESTATION OF GREATER GERBILS, ESPECIALLY BY IMMATURE H. IMPELTATUM S. & S.[1]

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INTRODUCTION

The Egyptian greater gerbil is so common in a certain narrow area of Egypt heavily populated by people and domestic animals and is so consistently and heavily parasitized by immature *Hyalomma impeltatum* during the warmer months of the year that it occupies a special niche of its own in the study of host-parasite relationships in Egypt. Methods used in the present project have been described by Hoogstraal and Kaiser (1957a).

THE HOST

The Egyptian greater gerbil, *Gerbillus* (*Gerbillus*) *p. pyramidum* Geoffroy, occurs in a specialized though extensive ecological zone in and beside the Nile Valley and much of the Delta for the entire length of Egypt. It burrows in palm groves, sandy cultivated patches, and newly reclaimed desert areas. In such situations, this gerbil is frequently the most common rodent and is in close association with dense concentrations of people and domestic animals resting, playing, and laboring over and around its burrows. It does not inhabit older silted farmlands, saline areas, extreme desert or semi-desert areas away from cultivation, or the littoral desert. Burrows of the greater gerbil are usually patently slightly moist. [A seasonal study of temperature and humidity conditions in these burrows, correlated with seasonal fluctuations of ectoparasite populations, is at present being undertaken by Mr. C. Yunker of this department and will be reported subsequently].

Collecting localities in Giza Province were Kafr Hakim, El Mansuriya, Manshiyet Radwan, Abu Rawash, Zawyet Abu Sallam, Dashur, Giza, Sakkara, Shubramont, El Katatba, Giza Pyramids, Kirdasa, Birqash, Ausim, and Abu Ghaleb. In Fayum Province, Kafr Mafuz was a collecting locality. All villages are within sixty miles of Cairo.

TABLE 1

MONTHLY DATA FOR INFESTATION BY NYMPHS OF *H. impeltatum*

MONTH HOST COLLECTED	NUMBER HOSTS	*H. impeltatum* REARED			AVERAGE PER HOST
		Males	Females	Total	
Jan.	1	1	0	1	1 00
Feb.	1	1	0	1	1 00
Mar.	3	1	4	5	1 66
Apr.	3	5	4	9	3 00
May	8	7	29	36	4 50
Jun.	36	81	91	172	4 78
Jul.	15	41	54	95	6 33
Aug.	20	67	88	155	7 75
Sept.	21	127	155	282	13 43
Oct.	32	77	83	160	5 00
Nov.	6	9	16	25	4 17
Dec.	3	4	2	6	2 00
Total	149	421	526	947	

Adult ticks reared from nymphs that detached in the laboratory from 152 hosts infested in nature were:

	Males	Females	
H. impeltatum	421	526	
H. dromedarii	13	14	
H. excavatum	1	0	
Total	435	540	(975 ticks)

Records of larvae and nymphs that did not molt to adults were not associated with the present

[1]Research Report NM 005 050.39.55. The opinions and assertions contained herein are the private ones of the authors and are not to be construed as official or reflecting the views of the Navy Department or the naval service at large.

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[2]With the technical assistance of Sobhy Gaber.

data, *i.e.*, the total infestation is significantly higher than indicated by the above figures.

Hyalomma impeltatum SCHULZE AND SCHLOTTKE
Kratz's Hyalomma

Nymphs from 152 *G. p. pyramidum* from the Cairo area were reared to adult ticks, chiefly between 7 October 1954 and 1 March 1956. One hundred and forty-nine hosts were infested by nymphal *H. impeltatum*, either together with or without other species, and 3 were carrying only nymphs of *H. dromedarii*. Of the 149 *impeltatum*-infested gerbils, 130 bore no other species, 18 also yielded nymphs of *H. dromedarii*, and one was parasitized by a single nymph of *H. excavatum* (Table I).

Tick-infested gerbils were sought throughout the entire year. In wintertime, an even greater number was examined than during other seasons. The few hosts found during winter indicate not only the low infestation per host but also the paucity of tick-infested individuals in the local gerbil population at this time. Records of non-infested hosts were not retained, these will be kept in the present extension of this research.

Nymphs dropped from the host 1 to 10 days, usually from 2 to 4 days, after having been brought from the field. A single, notable exception is represented by host number 50 collected on 21 November 1954, whose four nymphs detached 51 days later, on 11 January 1955. These long-feeding nymphs molted to normal adults, in the usual period of time, on 2, 7, and 14 February 1955.

The interval between detaching and molting to adults was extremely variable, even among nymphs that dropped from one host on the same day. During warmer months, this period was usually 16 to 22 days although it sometimes extended to 32 days. In fall, winter, and early spring it varied from 22 to 112 days, with 5 to 7 weeks being most common.

It should be noted that of the 947 ticks reared to adults, 421 (44%) were males and 526 (56%) were females. The interval between detaching and molting was no different for the two sexes.

Hyalomma dromedarii KOCH
The Camel Hyalomma

Twenty of the 21 gerbils yielding *H. dromedarii* were infested by only 1 or 2 nymphs of this species, and a single host bore 3 nymphs that were reared to adults. Eighteen of the same hosts were also parasitized by nymphs of *H. impeltatum*. The months of host collection are May (3), June (7), August (3), September (3), and October (5). Thirteen males and 14 females of *H. dromedarii* were reared from these 21 hosts. Camels, the chief host of the adult stage of *H. dromedarii*, are common in the areas inhabited by the greater gerbil.

OTHER *Hyalomma* SPECIES

A single male *H. excavatum* Koch was reared from a nymph from one of the hosts in this series.

The absence of infestation by immature stages of certain *Hyalomma* species found as adults on domestic animals that graze, rest, or pass by burrows of greater gerbils, and of other hyalommas whose immature stages infest small vertebrates in the same area should be noted. These are *H.* sp. no 1 near *excavatum*, *H. anatolicum Koch* (*sensu* Schulze) (=*H.* sp. no. 2 near *excavatum*), and *H. rufipes*.

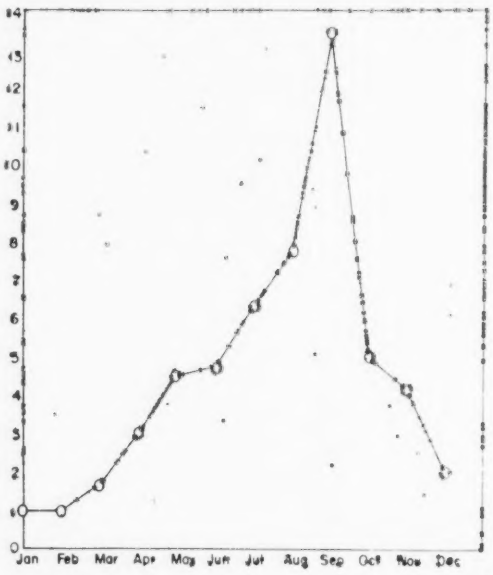

FIG. 1.—Average monthly incidence of nymphs of *H. impeltatum* on single hosts (*Gerbillus* (*G.*) *p. pyramidum*).

DISCUSSION AND CONCLUSIONS

Large populations of the Egyptian greater gerbil, *Gerbillus* (*G.*) *p. pyramidum* are restricted to palm groves and non-saline cultivated sandy patches in and beside the Nile Valley and Delta for the entire length of Egypt. Between May and October, greater gerbils infested by nymphal *Hyalomma impeltatum* S. & S. are easily found. During the cooler months, November through April, assiduous search reveals fewer host gerbils, all lightly infested by the same parasite. Approximately 14 percent of these hosts were infested by 1 to 3 nymphal *H. dromedarii*, and a single *excavatum* was also reared from the same group of animals. Four other *Hyalomma* species occuring in the same area on other animals are not known to parasitize the greater gerbil during any period of their life cycle. This form of gerbil,

therefore, is considered an important host only of immature *H. impeltatum* and to a much lesser extent of *H. dromedarii*.

The seasonal average incidence of nymphal *impeltatum*-infestation of greater gerbils is lowest from December through April (1 to 3 per host), gradually rises through August (up to 7.75 per host) reaches an extreme peak in September (13.43 per host), and drops greatly in October and November (5.00 and 4.17 per host) (fig. 1). The incidence of larvae and nymphs per host was actually higher than indicated by these figures; these records include only nymphs that detached and were reared to adults. Larvae were not reared and nymphs that died before molting were not counted.

It is of considerable interest that 44% of the adult *H. impeltatum* reared from nymphs from these gerbils were males and 56% were females. Exactly the same sex ratio obtained in our rearings of *H. rufipes* from migrating birds (Hoogstraal and Kaiser 1957b) though the point was not stressed in that report because of the smaller total number of reared ticks involved.

The site of attachment of *Hyalomma* larvae on the greater gerbil is invariably the host's ears while nymphs attach both to the ears and neck. Hosts displayed no effort to dislodge the parasites and we observed no great loss of ticks due to the gerbils' alarmed activities during and after capture.

SUMMARY

The Egyptian greater gerbil, *Gerbillus* (*G.*) *p. pyramidum* Geoffroy, large populations of which inhabit palm groves and sandy cultivated patches in and beside the Nile Valley and Delta of Egypt, is an important host of nymphal *Hyalomma impeltatum* Schulze and Schlottke. Nymphs from 149 of these hosts in the Cairo area molted to 121 males (44%) and 526 females (56%) of *H. impeltatum*. The seasonal average infestation is very low in winter, gradually rises to over 7 per host in August, reaches a peak of 13.43 per host in September, and falls sharply afterwards. The interval between nymphal detachment and molting to adults in the laboratory is variable in summer (generally 14 to 22 days; rarely up to 32 days), and extremely so during other months of the year (22 to 112 days).

A small proportion of the same hosts were infested by fewer nymphs of *H. dromedarii* Koch; and a single nymph of *H. excavatum* Koch, was also reared to an adult.

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1957b. *Idem.* 2. Parasitism of migrating birds by immature *H. rufipes* Koch. Ann. Ent. Soc. America 51 (1): 12–16.

BAT TICKS OF THE GENUS ARGAS (IXODOIDEA, ARGASIDAE).

3. THE SUBGENUS CARIOS, A REDESCRIPTION OF A. (C.) VESPERTILIONIS (LATREILLE, 1802), AND VARIATION WITHIN AN EGYPTIAN POPULATION[1, 2]

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INTRODUCTION

The much-mooted name *Argas vespertilionis*, originally applied in the genus *Carios* to an engorged specimen from bat haunts in France, accompanied an original description that is not sufficiently definite to verify the identity of the arthropod to which it refers. However, since only a single *Argas* species is known to parasitize European bats north of southern Italy and this name has long been in common usage, its retention appears probably to be warranted.

During the past several years the writer has studied most of the material of the *A. vespertilionis* group available in major collections throughout the world and has collected and reared hundreds of specimens from Egyptian populations. From this survey a number of basic facts and conclusions emerge:

(1) No differences between Egyptian and European populations can be ascertained at the present time.

(2) Material from the Ethiopian Faunal Region falls within the range of variation of populations in the Palaearctic Faunal Region.

[1]Research Report NM 005 050.29.33. Accepted for publication March 19, 1957.

[2]The opinions and assertions contained herein are the private ones of the author and are not to be construed as official or reflecting the views of the Navy Department of the naval service at large.

Although superficial differences in facies in series from the former area suggest that one or more separate species may have evolved in Africa south of the great deserts, available specimens are not numerous enough to support or deny this possibility.

(3) Essentially the same is true of material from the Near East to the Far East, with the exception of *A. pusillus* Kohls, 1950, from Palawan, Philippine Islands, which appears to be a valid species in the *A. vespertilionis* group.

(4) Attempts to differentiate larvae of this group into species on the basis of body shape of wild specimens taken from bats (Schulze 1930, 1936) are wholly worthless because of distortion, obscuring of salient features, and frequent mutilation of critical characters during removal from the host.

(5) With numerous samples from a large population now available, it appears that the best point of reference for recognition of *A. vespertilionis* is a description of specimens from caves at Abu Rawash, Giza Province, Egypt, together with observations on variation within this population.

The last point, then, is the object of this paper. With such criteria, the identity of other populations may be more easily established. Large series, however, will probably always be necessary before additional new species can be designated in this group.

While it would be timely to designate a neotype for *Argas vespertilionis* (Latreille), it appears advisable to propose that this be selected, after thorough study, from French populations of this tick.

Subgenus **Carios**

Parasites of which bats are hosts of predilection. Body flat, outline circular or subcircular; with a complete sutural line (lateral suture), with "celled" body periphery dorsally and ventrally, and with ventral "paired organs"; lacking appendagelike hood although body margin may be slightly expanded anteriorly. Integument finely wrinkled and granulated; discs distinct, arranged in clearly radiating rows. Mouthparts near anterior body margin. Legs moderately short and stout, arising far anteriorly; tarsal protuberances lacking.

Type of the subgenus. Caris vespertilionis Latreille, 1802. Type material lost (M. Andre, correspondence 1957). This subgenus also includes *A. pusillus* Kohls, 1950, and probably several other forms very closely resembling *A. vespertilionis* in various parts of the Old World. None is known from the Americas. *A. steini* Schulze, 1936, described from a larva from a "flying fox" in Timor, may be the third described species in this subgenus; this assumption is based merely on its far-flung geographical location.

The type species of the genus *Argas* is *A. reflexus* Fabricius, 1794.

Argas (Carios) vespertilionis (Latreille, 1802)

The Round Bat-Argas[3]

Figs. 1 to 23

Carios gen. nov. Latreille, 1796, p. 177, briefly described, without species designation, from a single larva found on a "noctule" bat by the author in France.

Caris vespertilionis Latreille, 1802; pp. 67–68; briefly described as above and from same material; generic spelling changed without indication of reasons for so doing (?misprint). Type material lost.

Acarus fischeri in Savigny, 1826, Plate IX, Fig. 6 (1, 1', 2, 2') [reproduced in present paper] of large nymphs or adults from Egypt (see next paragraph).

Argas fischeri Audouin, 1827, p. 427, description of material [illustrated by Savigny (1826)] may refer to large nymph or adult. These are the first definitely recognizable descriptions and illustrations referring to a known population of this species or group. If it is subsequently shown that Egyptian populations differ from those in Europe the name *A. fischeri* will have priority for Egyptian specimens. Also, if European and Egyptian populations are subsequently confirmed as representing one and the same species but objection is raised to use of the name *A. vespertilionis* because of the ambiguous nature of the original description, the name *A. fischeri* Audouin, 1827, will have priority.

Argas pipistrellae Audouin, 1832, v. 5, pp. 412–414, well described and figured (Plate 14, figure 1a to 1e) from larvae from "*Vespertilio pipistrellae*" in France; admits the possibility that this material may equal *Caris vespertilionis* Latreille, 1802.

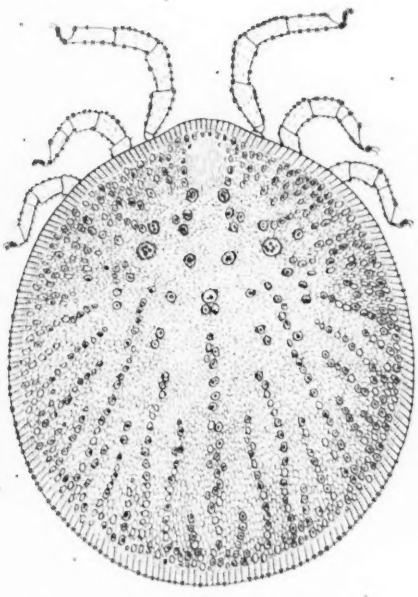
Argas vespertilionis (Latreille, 1796), Neumann, 1896, pp. 19–23; 1901, p. 254. First descriptions in modern sense. However, these descriptions and none by subsequent authors are anywhere near complete enough to provide criteria for separating this from related forms.

Argas vespertilionis (Latreille, 1796), Nuttall, Warburton, Cooper, and Robinson, 1908, pp. 31 to 39, Figs. 48 to 57; Plate I, Figs. 4 and 5. Synonymy and descriptions [in part confused with *A. confusus*; see Hoogstraal (1955, p. 586)].

Carios vespertilionis Latreille, 1796, Pospelowa-Shtrom, 1946, p. 5.

[3] *Acarus testudo* Risso, 1790, p. 239, is so poorly described that one has no assurance that it is a tick, let alone any certain species of tick. Although Oudemans (1929) considers this to be a prior name for *A. vespertilionis*, we have no recourse but to refer to this name as a *nomen nudum*.

For a view on the status of separate genera vs. subgeneric classification in the genus *Argas*, see Hoogstraal (1957).



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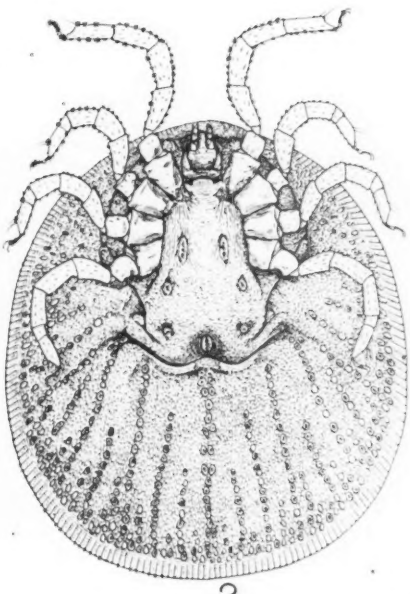

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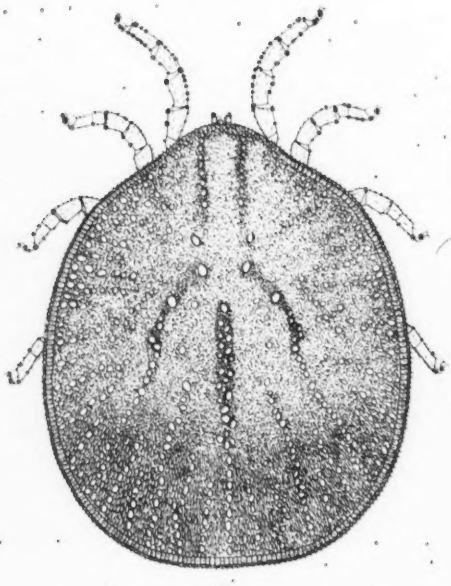

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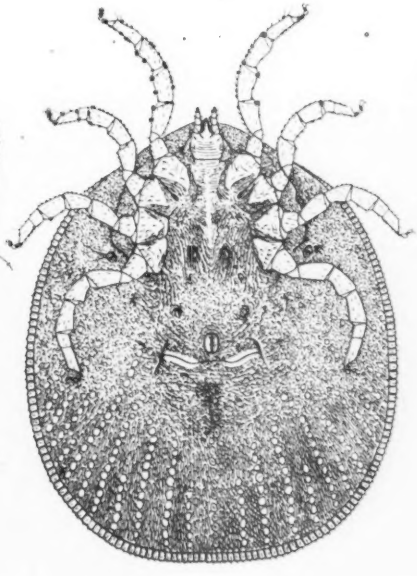

4

Abu Rawash population of *A.* (*C.*) *sexpertitionis*. FIGS. 1, 2. Female dorsal and ventral views. FIGS. 3, 4. Nymph, dorsal and ventral views. FIG. 5. Nymph, hypostome, ventral view.

REDESCRIPTION (OF POPULATION FROM ABU RAWASH, IMBABA, GIZA PROVINCE, EGYPT)

FEMALE: Measures from 4.2 to 6.0 mm. in length and from 3.8 mm. to 5.4 mm. in width; average specimen 4.8 mm. long and 4.4 mm. wide. *Body* (unengorged) thin and flat, concealing mouthparts but less than basal half of legs. *Outline* very variable (figs. 10 to 17); usually subcircular with width equalling at least four-fifths of length; lateral margins convex, posterior margin bluntly rounded, anterior margin somewhat more sharply rounded than posterior margin and slightly expanded over mouthparts (this expansion may be absent, when present it should not be confused with a hood). Outline less commonly (especially among smaller specimens) more subquadrate with subparallel lateral margins and more gradually rounded anterior and posterior margins. *Color* (unengorged) pale yellow to brownish, (engorged) reddish brown to black.

Dorsal integument consisting chiefly of fine wrinkling on central anterior area with low, flat granulations towards margins and with similar granulations posteriorly; granulations subcircular to subovate, only slightly elevated, tending to

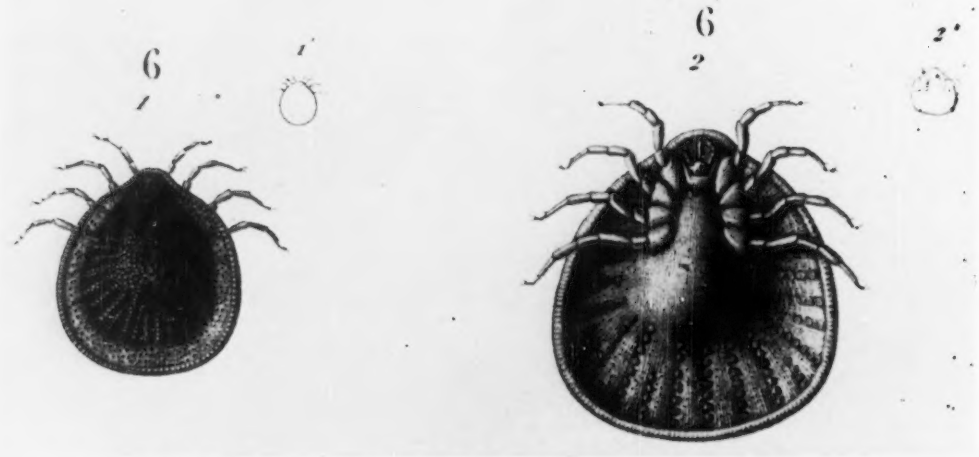

FIG. 6. Original illustrations of *A. fischeri* from Egypt in Savigny (1826). (Dorsal and ventral views of large nymph or female).

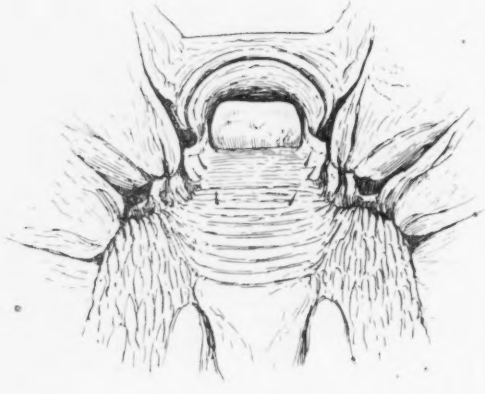

FIG. 7. *A. (C.) vespertilionis*, female, genital area.

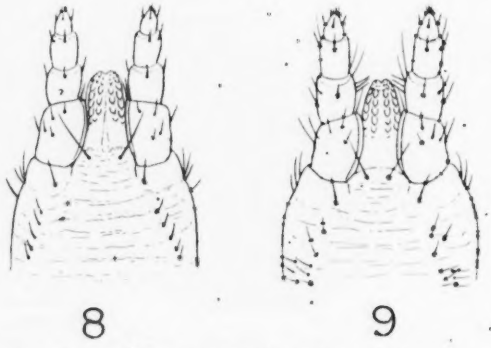

FIG. 8. *A. (C.) vespertilionis*, male, capitulum, ventral view. FIG. 9. Same, female, capitulum, ventral view.

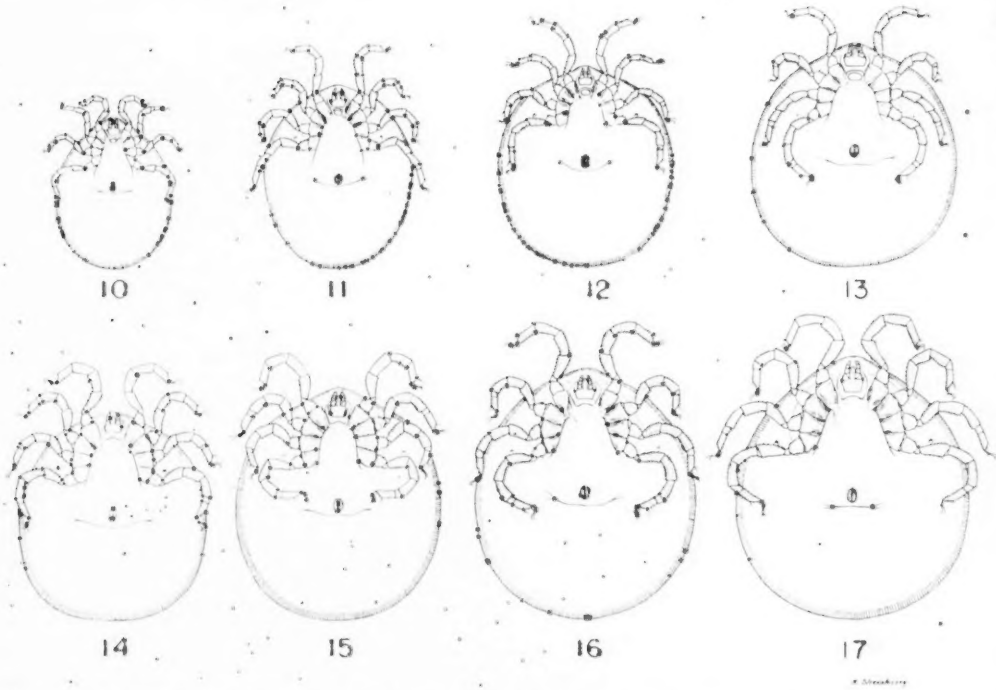

FIG. 10-17. Variation in size and shape among Abu Rawash population; specimen for fig. 17 measures 6 mm. in length; 10 to 13 (♂♂); 14-17 (♀♀).

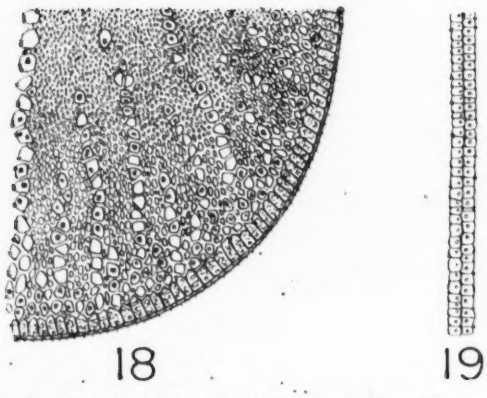

FIG. 18. *A.* (*C.*) *vespertilionis*, female, dorsal integument, lower right quadrant. FIG. 19. Same, lateral integument.

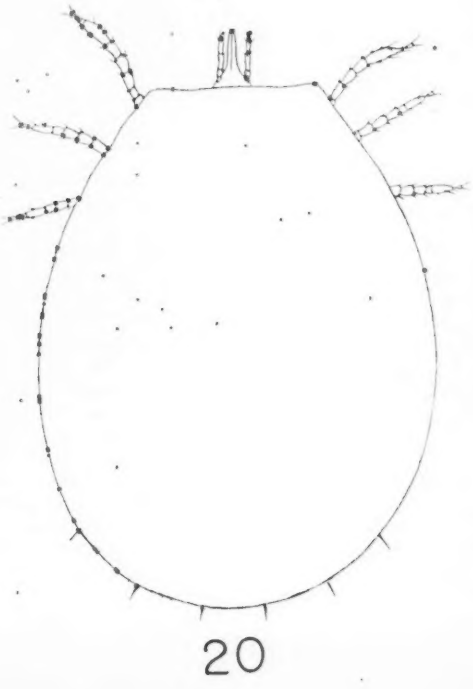

FIG. 20. *A.* (*C.*) *vespertilionis*, larval outline, fully engorged.

become slightly larger towards margin, becoming smaller, finer, and less elevated anteriorly, thus giving a finely "wrinkled" appearance; lateral margin with distinct, quadrangular "cells" delineated by narrow, deep, parallel grooves. *Discs* distinct and in definitely radiating rows (in black, engorged individuals discs are easily seen when specimen is held obliquely to source of light). *Lateral integument* with "cells" from dorsal and ventral surface interrupted by sutural line (lateral suture) that completely encircles body. *Ventral integument* similar to that of dorsum; discs also in clearly radiating rows; with four pairs of buttons, one just beside coxae IV, one just posterior of coxae IV, one level with anterior margin of anus, and one just laterad of the third pair in termination of supracoxal fold and therefore frequently concealed. *Hood* absent. *Hairs* minute, one arising from each marginal "cell"; more numerous on anterolateral margin though frequently rubbed off.

Eyes absent. *Spiracular plates* small, situated lateral to coxae IV. *Genital aperture* a deep, narrow, transverse slit closely confined laterally by coxae I and anteriorly by a "fleshy ridge" separating it from camerostome; posterior lip in shape of mild arc not as wide as aperture itself. [The close confinement of the genital aperture is unique in the genus; in unmated specimens it may appear as a deep groove posteriorly bordering the fleshy ridge bounding the camerostome—such specimens might be confused with nymphs; in mated individuals the separated lips of the aperture are more distinct]. *Anus* elliptical, situated at midlength of body; each valve with at least three pale hairs. *Ventral paired organ* consisting of two curved apertures with finely striated lips, situated immediately posterior of anus. *Ventral grooves* absent; *coxal* and *supracoxal folds* present though more or less definite.

Legs arising from anterior third of body; moderately long and stout. *Coxae* contiguous,

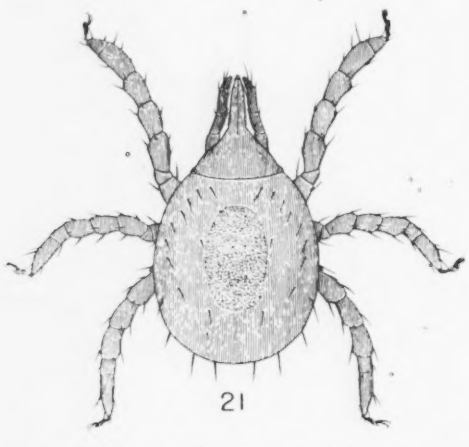

FIG. 21. *A. (C.) vespertilionis*, larva, unengorged, dorsal view.

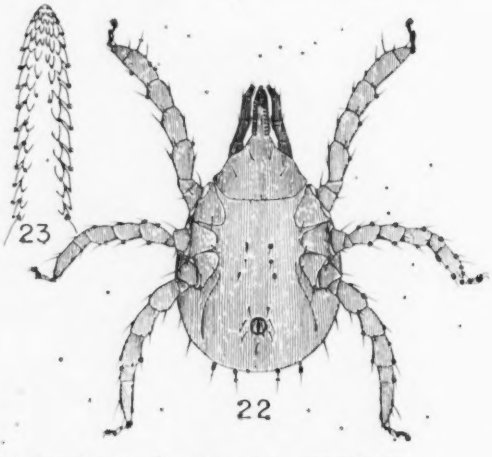

FIG. 22. Same, ventral view.

FIG. 23. Same, hypostome, ventral view.

Capitulum in fairly deep camerostome closely bounded by coxae I, from which it is separated laterally and posteriorly by a "fleshy ridge". *Basis capituli* ventrally with convex lateral margins, three pairs of sublateral hairs basally, and a submedian line of approximately seven hairs extending from base to apex. *Hypostome* slightly over twice as long as wide; apex deeply emarginate, with a very weak corona; dentition 2/2 in files of six or seven denticles (one or two files of extremely weak submedian denticles rarely also present); a pair of posthypostomal hairs arising level with base of palpi and extending to level of midlength of basal palpal segment. *Palpi* extending beyond apex of hypostome by full length of segments 3 and 4; segments 2 and 3 subequal, each two-thirds length of segment 1; segment 4 approximately half length of 2 or 3.

variously tapering. *Tarsi* lacking dorsal protuberances; I may be very slightly elevated over haller's organ; I dorsally truncate subapically, thence gradually tapering; II and III more or less gradually tapering; IV gradually tapering. *Pads* small. *Claws* moderately long but delicate, subequal.

MALE: Similar to female except for smaller size and difference in genital aperture. Measures from 3.6 mm. to 4.8 mm. in length and from 3.2 mm. to 4.4 mm. in width; average specimen 4.5 mm. long and 4.0 mm. wide. *Genital aperture* situated between coxae I, with a rectangular flap bounded anteriorly by a semicircular "fleshy ridge" and posteriorly by an area of transversely wrinkled integument. *Hypostome* similar to that of females except that the denticles and corona are slightly weaker and the incidence of a very

few, weak submedian denticles on the shaft is somewhat higher.

NYMPH: Closely resembling adults except for size, although large nymphs may equal all but large females. Small nymphs frequently are more narrowly elongate than adults and resemble *A. persicus* in outline. The wrinkled area of the dorsal integument is somewhat more extensive. The "ventral paired organ", lateral suture, and marginal cells are also present in this stage. *Capitulum* situated in camerostome at level of anterior half of coxae I and bounded by "fleshy" ridge; *palpi* often partially extending beyond anterior margin of body. *Hypostome* similar to that of adults except that the apex is only slightly or not emarginate, the denticles of the corona are comparatively somewhat stronger, and the external file of denticles is situated more laterally. *Tarsi* usually more abruptly tapered than in adults.

LARVA (UNENGORGED): Measures approximately 0.8 mm. from apex of hypostome to posterior body margin; color pale white; mouthparts arising from anterior margin of body; lateral margins of body convex, posterior margin gradually rounded. An elongate oval squamous shield on dorsum. *Hairs* on body numbering approximately four pairs laterally and sublaterally on posterior margin; eight sublateral pairs and two or three submedian pairs on dorsum; three submedian pairs on venter between coxae II and III, and three or four pairs closely surrounding the anus.

Hypostome from basal denticle four times as long as greatest width; gradually tapered anteriorly with a small but definite corona; dentition 2/2 for length of shaft and 4/4 anteriorly; a pair of lateral and submedian files of approximately twelve denticles each extending from base to apex; an inner pair of files of approximately five denticles each extending less than half length of shaft; frequently one (rarely two) submedian pairs on anterior fourth of shaft. [This same type of dentition is referred to by Nuttall *et al.* (1908) as 4/4]. Posthypostomal hairs small; two pairs anterior of which does not extend beyond apex of basal palpal segment. *Palpi* extending to apex of hypostome, narrow; segments 1 and 4 short, 2 and 3 longer and subequal.

Anus situated half way between level of base of coxae III and posterior margin, with a long hair from each valve.

Legs moderately long and narrow. *Coxae* partially contiguous, progressively larger from III to I. *Tarsi* I and III gradually tapered, II slightly more abruptly tapered; lacking dorsal subapical protuberances; pads relatively large; claws small.

LARVA (ENGORGED): Body shape becomes more and more elongate and anterior margin more and more truncate as engorgement progresses; anterior margin may more or less overlap mouthparts but usually does not do so; legs not concealed. In some specimens the body outline may be wider than typically when fully engorged. The hairs are frequently rubbed off and the coxae are separated from each other by integument.

DISCUSSION AND CONCLUSIONS

Variation in the Abu Rawash population: The body outline of individual specimens of *A. vespertilionis* from the Abu Rawash population (figs. 10 to 17) is more variable than I have seen in any other species of this genus. Other Egyptian populations of this tick are equally inconsistent in this feature. None of the bat hosts of these populations are known to migrate great distances though they do move about from locality to locality within Egypt.

In several series of fewer specimens from various parts of the world, each sample displays a more consistently uniform and characteristic body outline. Statistical data for an arbitrary number of specimens, as twelve, from such widely scattered localities as England, Egypt, Belgian Congo, Union of South Africa, and India might have proven to be thoroughly convincing for separating species on the basis of body outline, a fairly constant character among other *Argas* species.

If only equally small series from Egypt had been studied, we should have concluded that subcircular body outline and size typical of the majority of available specimens represent valid species criteria for Egyptian populations, which we have previously referred to (though not in publications) as *A. fischeri*. However, among hundreds of specimens from Abu Rawash, some five percent of females and fifteen percent of males are sufficiently non-typical in body outline (compare figures 10 and 11 with 13 and 17) to indicate that these are merely intraspecific variants. Every stage of gradation is observed in large series from a single cave at Abu Rawash.

No other adult or larval characters have yet been found to differentiate European, Egyptian, tropical African, and southern African specimens of this tick. We therefore refer to populations from both continents as *A.* (*Carios*) *vespertilionis* (Latreille, 1802) though acknowledge the possibility that more than a single species may eventually be proven from these continents.

As already stated, it is desirable that larger numbers of European and African specimens of this tick be compared, and that a neotype be selected from French populations. If European and Egyptian populations are shown to differ, the name *A. fischeri* Audouin, 1827, has priority.

Biology: The life cycle and biology of Egyptian populations have been reported by Hoogstraal (1956, pp. 106–109). More recent data indicate that laboratory-reared females lay three of four batches of from 35 to 50 eggs over a twelve month period, commencing no less than thirteen weeks (previous data indicated no less than six months)

after having molted to the adult stage and only after two blood meals as an adult. Certain egg batches were deposited three months apart without an intervening blood meal although usually oviposition followed blood meals by about one week. Males and females were placed together a few days after molting and maintained together as a single pair through the entire period of study.

ACKNOWLEDGMENTS

I am grateful to Glen M. Kohls not only for reviewing the manuscript but also for suggesting some years ago that because of our fortunate position in Cairo we were particularly well situated to undertake biological and systematic studies of the Argasidae; also to Dr. C. B. Philip for reviewing the manuscript. The warmest thanks are also due Dr. G. Owen Evans for considerable assistance in finding and checking rare old literature during two visits to the British Museum (Natural History).

SUMMARY

Both sexes and immature stages of *Argas* (*Carios*) *vespertilionis* (Latreille, 1802) are described from populations from bat-infested caves at Abu Rawash, Giza, Egypt, and the subgenus *Carios* is defined. Considerable variation in size and body outline of individuals in the Abu Rawash population, and inability to discern critical differences between these and fewer numbers of specimens from elsewhere in Africa and Europe, cause us to consider these as a single species. Material from the type locality in France should be collected in larger numbers for comparative purposes, and a neotype should be designated from French populations. If Egyptian and European populations eventually are shown to differ, the name *A. fischeri* Audouin, 1827, is available for the former.

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NEW PUBLICATIONS

Index XV to the Literature of American Economic Entomology, 1955, and the 12th Edition of the Pest Control Directory, Entoma, 1957–1958 are now available. All entomologists need these publications for ready reference.

LOW TEMPERATURE STUDIES ON THE ISOLATED HEART OF THE BEETLE, POPILIUS DISJUNCTUS (ILLIGER)[1]

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ABSTRACT

The effects of brief and extended treatments at subzero temperatures have been studied using the isolated heart of the beetle *Popilius disjunctus*. This preparation is especially favorable for low temperature studies in that it can be maintained *in vitro* for periods up to 33 hours and provides several criteria for quantifying injury. In insect Ringer approximately one third of the hearts exposed at −6° to −8° resumed contraction after thawing, but none recovered after exposure at −20°. Glycerol in concentrations of 5% to 30% protected hearts exposed at −20° for 18 hours, with greatest protection at 5% and 10% glycerol. Glycerol concentrations of 0.1% and 1% were ineffective. In 10% glycerol-Ringer hearts showed a high percentage survival at −18° to −20° through 11 days storage but a marked decrease in survival after 15 and 20 days storage. In contrast to results of others on vertebrate material, recovery never occurred after brief exposures at −70° to −76° regardless of concentration of glycerol or rate of freezing and thawing. As the period of storage was increased from 1 to 20 days progressive changes were found in three parameters of heart activity after thawing: (1) the period of survival *in vitro* decreased; (2) the rate of contraction decreased; and (3) the time before the resumption of contraction increased. The effects of storage have been considered in terms of the continuation of chemical reactions at subzero temperatures and the preferential inhibition of certain reactions resulting from differences in temperature coefficients.

Injury from low temperature may be expected to be graded rather than all-or-none. In a particular experimental system, however, injury may appear graded or not depending upon the criteria of effect. At the level of the single cell one could anticipate that with suitable measurements a gradation of effects would be demonstrable through an examination of various parameters of cellular activity. At the tissue or organ level a system favorable for the study of cold injury would also be one showing several criteria of injury, each of which could be quantified.

The isolated heart of the beetle *Popilius disjunctus* is a convenient experimental material which meets this requirement and has therefore been employed in the present study. As an *in vitro* coordinated rhythmic system it provides criteria which are considerably more delicate than survival alone. The criteria of cold effects other than survival include: (1) rate and strength of beat; (2) period of survival *in vitro*; (3) coordination of contraction; and (4) length of time between thawing and resumption of contraction.

The two main problems examined in this study are the effect of the medium on resistance to subzero temperatures and the influence of time of storage at low temperature on the character of later contraction. Special attention has been given to the protective action of glycerol (Maximov, 1912) which in recent years has been studied extensively on vertebrate material (see Smith, 1954). The many studies on the resistance of insects to low temperature (see Payne, 1927; Belehradek, 1935; Bucher, Cameron, and Wilkes, 1948) have for the most part been concerned with intact organisms, but the isolated insect heart has also been studied from this point of view (Walling, 1906; Asahina, Aoki, and Shinozaki, 1954).

METHODS

Adult specimens of the beetle *Popilius disjunctus* (Illiger) were collected in rotting hardwood logs near Durham, N. C. and kept in the laboratory in moist pulverized wood from the same logs. Normally beetles were used within a week after collection. The experiments were carried out during the months of May to September, 1956 and 1957. Room temperatures during this period were 24.5° to 32.2° C.

The heart was isolated by severing the beetle behind the prothorax, removing the elytra and hind wings, and clipping free the dorsal abdominal wall to which the heart is attached. Four heart preparations were fastened with steel pins to a layer of paraffin 4 mm. in thickness in the bottom of a petri dish 50 mm. in diameter and covered with 15 ml. of insect Ringer containing bicarbonate (Gaulden and Carlson, 1951). The Ringer and all experimental solutions in Ringer were adjusted to pH 6.7. Aeration of the hearts was provided by playing a gentle jet of air on the surface of the solution. This raised the pH to 7.2. Solutions were renewed on the hearts every 2 hours. Approximately 975 heart preparations were studied.

Immediately after isolation and prior to experimental treatment each heart was observed with a dissecting microscope, the contraction rate determined, and the contraction characteristics recorded. Rate measurements were made on a particular segment, usually the third, since cold

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treatment not infrequently abolished coordination between segments, resulting in differences in rate in different portions of the heart. The strength of contraction was designated as strong, moderately strong, weak, or very weak and recorded at each observation. All final determinations of heart rate were carried out in a constant temperature bath at 31° with the exception of one series at 15.5° to 17°.

A variety of methods was employed in exposing isolated heart preparations at low temperatures and these will be mentioned under Results. In the standard procedure for the majority of the studies at −8° and −18° the hearts were pinned out in dishes as previously described. Each dish was covered to prevent evaporation and placed in a refrigerated chamber without special attention being given to the rate of freezing. At the termination of the low temperature treatment the hearts were quickly returned to 31° by first placing the dish in a bath at 40° and pouring solution warmed to 40° onto the frozen solution to bring about partial thawing. Thawing was completed by transferring the hearts to a larger dish of solution at 31° and replacing this almost immediately with fresh solution also at 31°. Contraction rates were taken at 2-hour intervals and the number of hearts showing contraction was recorded every 30 minutes.

RESULTS

Behavior of untreated hearts.—As background for the temperature studies, the behavior of the untreated heart of *Popilius disjunctus* will first be described briefly.

The isolated heart almost invariably exhibited a rhythmic and usually coordinated contraction which continued for periods up to 33 hours in aerated insect Ringer at 15.5°–17°, with an average time of 27.5 hours. At 31° the period of contraction averaged 12.7 hours, with a maximum of 16 hours. When the heart was isolated in a moist chamber without being placed in any medium, contraction continued for about 3 hours (28°–31.1°). That the hearts in Ringer functioned normally in pumping the surrounding fluid was shown by placing India ink at the open posterior end. It was immediately drawn inside and expelled anteriorly.

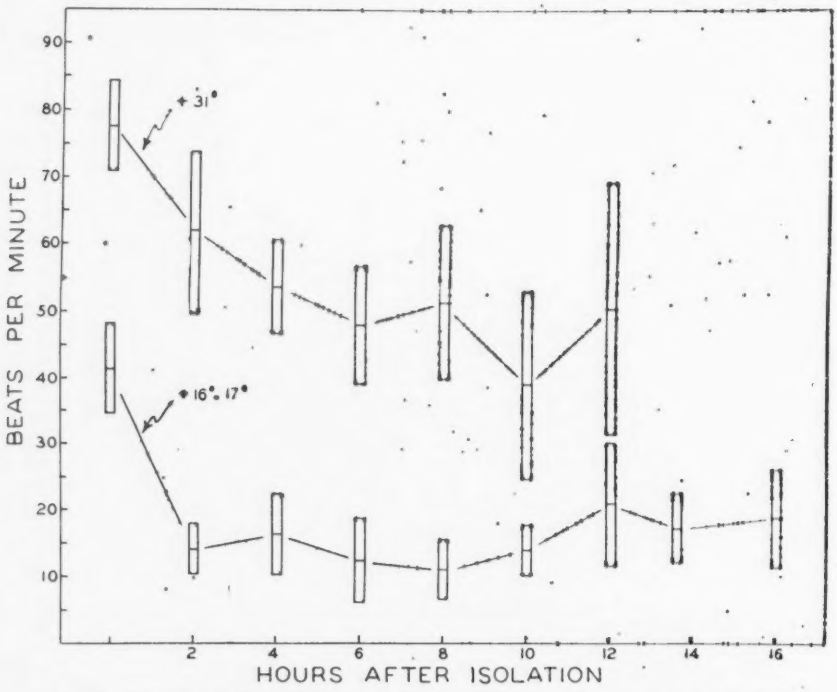

FIG. 1. Contraction Rates of Untreated IsolatedHearts. Mean rates and standard deviations shown. Twelve hearts observed at each temperature. Insect Ringer, pH 7.2

The isolated heart normally contracted vigorously for 4 to 6 hours after isolation. Thereafter the vigor gradually decreased. Under all conditions the contraction rate decreased from the rate observed immediately after isolation (Fig. 1). A similar decrease has been reported by Yeager and Hager (1934) in the isolated cockroach heart. Figure 1 shows the mean rates of contraction together with standard deviations for two sets of 12 hearts observed at 2-hour intervals, one set at

16°–17° and the other at 31°. The decrease from the initial rate and the decreased rate at lower temperature are clearly evident. The rate of contraction of individual hearts as determined by counts at 10-minute intervals fluctuated widely even at constant temperature, contrasting with Davenport's (1949) finding of a constant rate in the orthopteran *Stenopelmatus longispina*. The fluctuations in the Popilius heart were not evident when the rates were determined only at 2-hour intervals.

Survival at subzero temperatures.—Survival of isolated hearts has been studied under various conditions at temperatures of −6° to −8°, −18° to −20°, and −70° to −76°. The conditions

TABLE I

EFFECT OF GLYCEROL CONCENTRATION ON SURVIVAL OF HEARTS* STORED AT −20° FOR 18 HOURS

% GLYCEROL	% SURVIVAL
0.1	0
1.0	0
5.0	100
10.0	92
20.0	67
30.0	50

*Hearts isolated in Ringer and transferred to glycerol-Ringer solutions and immediately placed at −20°. Survival checked in Ringer. Twelve hearts used at each glycerol concentration.

have included exposures for short periods of time, storage for several days, and the effect of added substances on survival. After 3 hours storage at −6° to −8° about one-third of the hearts recovered. The temperatures lower than −8° were invariably lethal both to hearts exposed directly after isolation without added medium and to hearts in insect Ringer. The most obvious changes in those preparations which did not recover were marked contraction of the alary muscles and a shortening and curling of the entire preparation. Hearts treated with concentrations of glycerol of 20% or higher did not exhibit this curling even at the lowest temperatures.

Effect of glycerol.—Preliminary experiments with 10% glycerol in insect Ringer (v/v) demonstrated that this solution will protect hearts against the lethal effect of −8° and −20° for extended periods. The efficacy of glycerol was tested over a wide range of concentrations by exposing groups of 12 hearts at −20° for 18 hours and observing the resumption of contraction in Ringer (Table I). At this temperature solutions of glycerol of 20% and lower freeze solidly. Recovery was excellent in 5% and 10% glycerol and less at higher concentrations. Concentrations of 0.1% and 1.0% were ineffective. The decreased recovery in 20% and 30% glycerol does not necessarily indicate less effective protection against freezing *per se* but may result from an effect of the glycerol itself on contraction. This possibility is suggested by a progressive decrease in rate of contraction in increasing concentrations of glycerol and by the fact that 30% and 40% glycerol in insect Ringer will bring about a reversible cessation of contraction.

Ten percent glycerol in Ringer was selected as a medium for the study of the effects of low temperature storage. Others have found this concentration effective as a protective agent in low temperature studies on vertebrate material (Smith, 1954; Joyner and Bennett, 1956; and Pomerat and Moorhead, 1956). This solution maintained the contraction of untreated hearts for extended periods as shown in the upper curve in Fig. 2.

EFFECT OF STORAGE TIME AND STORAGE TEMPERATURE

The effect of the time of storage of the isolated beetle heart at low temperature can be expressed quantitatively in terms of three parameters: (1) the percentage of recovery; (2) the period of contraction *in vitro*; and (3) the period of time after thawing before the resumption of contraction. The decrease in rate of contraction following low temperature treatment can also be used, but this may be open to question as mentioned below.

Recovery.—Hearts treated with 10% glycerol-Ringer and stored at −8°, −18°, and −20° for periods through 11 days showed good survival (Table II), but after 15 and 20 days storage the percentage survival was low at −18° to −20°. These results might be taken to indicate that there is a critical period between 11 and 15 days. However, other effects of storage described below show that injury was progressive beginning with periods of storage of 1 day or less.

Period of survival.—The period which isolated

TABLE II

RECOVERY AFTER LOW TEMPERATURE STORAGE*

STORAGE TEMP.	1 DAY TOTAL	1 DAY RECOV.	5 DAYS TOTAL	5 DAYS RECOV.	10 DAYS TOTAL	10 DAYS RECOV.	11 DAYS TOTAL	11 DAYS RECOV.	15 DAYS TOTAL	15 DAYS RECOV.	20 DAYS TOTAL	20 DAYS RECOV.
−8°C.	44	43 98%	36	36 100%	16	16 100%	12	11 92%				
−18° to −20°C.	68	67 99%	60*	60 100%	28	23 82%	12	11 92%	12	3 25%	12	2 17%

*Pooled results of several experiments. Hearts stored in 10% glycerol-Ringer. Recovery observed at room temperature in 10% glycerol-Ringer.

hearts continued to beat after low temperature storage at −18° was inversely related to the time of storage (Fig. 2). If one selects arbitrarily the periods when 50% of the hearts are still contracting and plots these as a function of storage time, essentially a straight line relationship is obtained. With the longer periods of storage some of the hearts never resumed contraction, of course (*cf.* Table II).

Latent period of recovery.—A striking effect of low temperature on the isolated beetle heart was a delay in the resumption of contraction on return to room temperature. The duration of this latent period was found to depend upon both storage temperature and duration of storage (Fig. 3). For hearts at −18° the latent period was directly proportional to the storage time through 15 days. With fifteen days storage the latent period was more than 2 hours. The same general behavior was seen with −8° storage but the latent periods were shorter. The increased effect at the lower temperature is a point of special interest to be discussed later. The reliability of the points for 15 and 20 days of storage is open to question because of the small number of hearts that survived these periods. The change in slope observed beyond 15 days at −18° was also found with storage at −8° but after 5 days, as

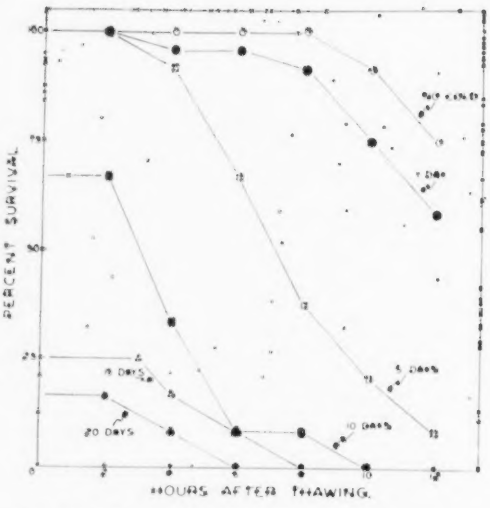

FIG. 2. Effect of Duration of Low Temperature Storage on Duration of Contraction. Storage temperature −18°. Medium 10% glycerol-Ringer. Twelve hearts used for each period of storage. Hearts maintained at 31° after thawing. Observations made every 30 minutes for as long as contraction continued but only 2-hour intervals plotted through 12 hours.

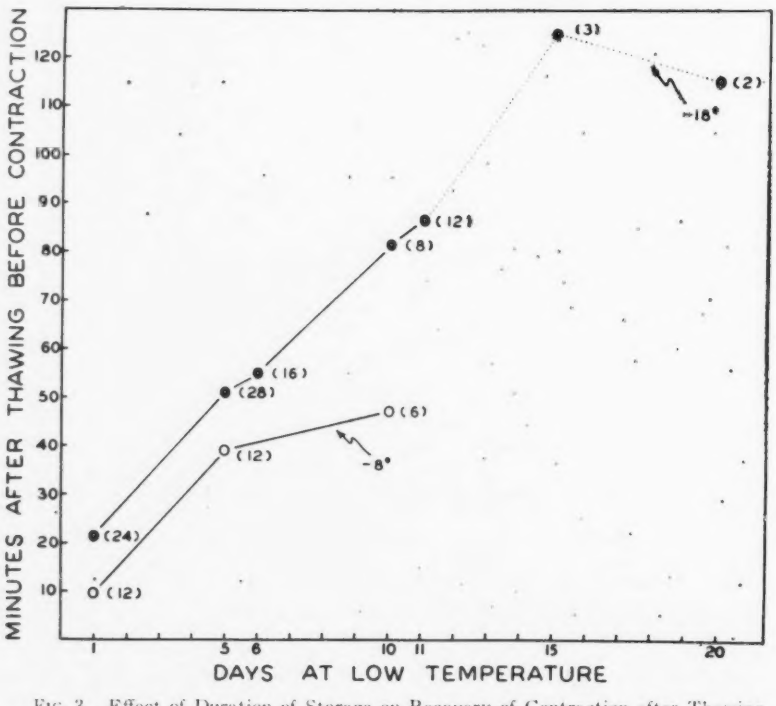

FIG. 3. Effect of Duration of Storage on Recovery of Contraction after Thawing. Points give mean rates for number of hearts indicated in parentheses. Hearts maintained at 31° after thawing.

shown in Fig. 3 and also in another series at −8° not shown.

Contraction rate.—The contraction wave of untreated hearts was usually coordinated, sweeping quickly from the posterior to the anterior end. After cold treatment reversal of heart beat was sometimes noted, and coordination was usually lost, one segment of the preparation showing a different rate from that of another. The first portion to resume contraction after thawing was frequently the most posterior; and and the aorta which is anterior was usually the last portion beating. In hearts stored for 10 days or longer, contraction may be limited to a single segment. Hearts, both untreated and

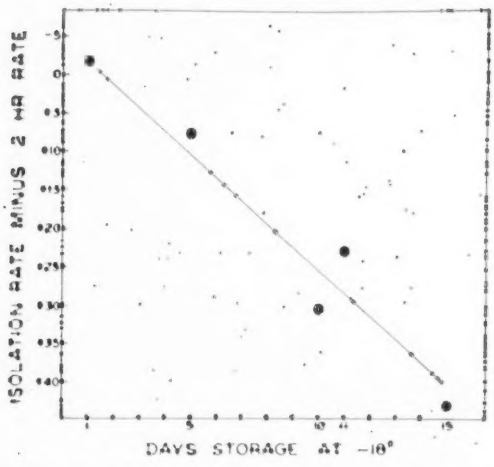

FIG. 4. Effect of Duration of Storage on Contraction Rate. Points represent mean change in rate between precold rate and rate two hours after thawing. Storage temperature −18°. Number of hearts observed: 4 day, 21; 5 days, 20; 10 days, 7; 11 days, 8; 15 days, 3. Heart rates determined at 31°.

after storage at low temperature, contract less and less strongly with time *in vitro* and then stop. Occasionally a temporary resumption of contraction will occur on the addition of fresh medium or blood.

The contraction rate bears an interesting relation to the time of storage, but only during the period soon after thawing. The rate two hours after thawing as compared with the rate before freezing decreased in proportion to the period of temperature treatment (Fig. 4). The overall pattern of change in rate with time for hearts exposed for various periods of storage was not greatly different from the pattern in untreated hearts; and the decreased initial rate after freezing may simply reflect the decrease with time characteristic of untreated hearts but greatly retarded. Accordingly, the change in contraction rate of cold-treated hearts cannot necessarily be attributed to an effect of low temperature *per se*.

EFFECT OF TEMPERATURES BELOW −20° C.

Several investigators have shown that through the use of glycerol various cells and tissues will recover after exposure to −76° or lower (see Smith, 1954; Joyner and Bennett, 1956). In the case of the beetle hearts recovery so consistently obtained at −18° to −20° never occurred at temperatures in the range −70° to −76° with any of the several experimental procedures employed. These included the use of 10%, 20%, 30%, and 40% glycerol-Ringer with both slow and rapid freezing. Thawing was always carried out rapidly with warmed solutions. In attempting to obtain recovery after slow freezing, hearts were immersed in 3 ml. of 10%, 20%, and 30% glycerol-Ringer in small test tubes and frozen to −72° at a rate of 1° per minute or less by placing the hearts in an insulated chamber surrounded by an alcohol-solid CO_2 mixture. Hearts were thawed quickly in warmed solution and observed in 10% glycerol-Ringer.

DISCUSSION

The effects of low temperature have been considered to be of two general types (Weiser and Osterud, 1945): immediate effects resulting directly from freezing and thawing, and effects of storage. Both types were shown by the beetle heart. Hearts were killed by short exposures to temperatures of −8° and lower in a Ringer medium and to temperatures in the range −70° to −76° in a glycerol medium. Studies relating to the effects of storage with a variety of organisms (Belehradek, 1935; Bucher *et al.*, 1948) permit the generalization that at moderately low temperatures (to −20°) the effects become more pronounced as the temperature is lowered and as the time of exposure is increased. Effects on the beetle heart stored for periods from 1 hour to 20 days follow this rule with respect to: (1) recovery after storage at −18° (Table II); (2) period of survival *in vitro* after thawing (Fig. 2); and (3) period required for resumption of contraction after thawing (Fig. 3).

The time for the resumption of contraction of the beetle heart bore a straight line relationship to the period of storage and was greater with storage at −18° than at −8°. One could postulate that this resulted from a progressive accumulation of material due to the preferential inhibition of a reaction(s) in a series having different temperature coefficients. Eventually an equilibrium condition would be reached and give a maximum effect as suggested by the leveling of the curves in Fig. 3. At the higher temperature (−8°) equilibrium could appear sooner, and an earlier leveling is seen in Fig. 3. The time for recovery of contraction would thus depend upon the elimination of accumulated material. With

storage of sufficient length at −18° to −20° an irreversible toxicity occurred. Accumulation of toxic material as a factor in cold injury of stored fruit has been advanced by Plank (1941; 1943) and by Smith (1947). Plank has suggested that reaction series of two types are involved, one leading to the accumulation of toxic material, the other to its metabolic removal. The amount of injury produced will be governed by the temperature coefficients of the reactions. If chemical reactions occurring at low temperature constitute a factor in injury, then at very low temperatures the effect of storage should decrease and disappear. This has been found for the bacterium *Treponema pallidum* (Weiser and Osterud, 1945) and for vertebrate material (Smith, 1950; Smith and Parkes, 1951; Scherer and Hoogasian, 1954).

If, in the recovery of the heart, respiratory reactions were limiting, the addition of respiratory substrates might be effective. However, the addition of sodium succinate, sodium pyruvate, or sodium alpha-keto glutarate in 10^{-3} M concentrations were without effect in changing the latent period of the resumption of contraction.

Progressive enzyme denaturation from increased salt concentration due to ice crystallization does not appear to be a likely cause of storage effects on the latent period since this would give curves of different form from those in Fig. 3, and the −8° curve would lie much above the −18° curve.

Glycerol protected the beetle heart against the lethal effect of temperatures down to −20°. This extends the protective action of glycerol to invertebrate material. The failure of glycerol to protect the insect heart against temperatures of −70° to −76° is a point of special interest. The concentrations of glycerol employed with the beetle heart (10%, 20%, 30%, and 40%) gave protection of vertebrate material at temperatures down to −190° (Smith, 1954), although not in all cases (Pomerat and Moorhead, 1956). Emphasis has been placed on the reduction of the salt concentration by glycerol as an explanation for its protective effect (Lovelock, 1953); and increase in intracellular salt is to be expected with extracellular ice formation (Asahina *et al.*, 1954). Also, glycerol will lessen mechanical damage due to extracellular ice crystallization (Smith, Polge, and Smiles, 1951). Intracellular ice formation may be involved as well. Asahina *et al.* (1954) have shown that the heart of the caterpillar *Cnidocampa flavescens* could withstand extracellular but not intracellular ice crystal formation. The isolated heart could survive much lower temperatures (to −20°) in the winter as compared with warmer seasons (to −5°); and this appeared to be correlated with the absence of intracellular crystallization in the winter forms. Results of this nature direct attention to the colloidal state of the protoplasm as a factor in resistance to cold injury. Temperatures of −6° to −8° were lethal for most beetle hearts during the summer months, which is in general agreement with the finding of Asahina *et al.* (1954).

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We wish to thank Dr. George W. Schwert for his helpful discussion of reaction kinetics.

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DESCRIPTION AND BIOLOGY OF HESPEROCIMEX SONORENSIS, NEW SPECIES, AN ECTOPARASITE OF THE PURPLE MARTIN (HEMIPTERA: CIMICIDAE)[1]

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ABSTRACT

This species is described from a population inhabiting nests of *Progne subis hesperia* in Sonora, Mexico. In laboratory studies it was found that first instar nymphs, fed once to repletion and then starved, molted and survived up to 63 days; that adults unfed after their final moult survived up to 169 days (males) or 218 days (females); and that a normally reproducing colony starved after approximately 75 days of age showed maximum survival for males of 59 days, for females 66 days. Well nourished virgin females were incapable of laying eggs, but after mating oviposited at the rate of 5.79 eggs per day per female for five consecutive weeks, with maximum production 6.88 eggs per day per female over a 3-day period. In one colony of 9 males and 14 females 5,195 eggs were produced over a 28-week period, an average of 343 per female, and 92.5% of these eggs hatched. Of 301 nymphs emerging to the adult stage, 37.9% were females, 62.1% males. Limited autogenous reproduction can occur in this species. In a colony where both sexes were not fed, 15 females produced 9 eggs; in another where only the females were unfed 13 females produced 25 eggs. Unfed males were found capable of inseminating females with viable sperm. 28 unfed males and 14 well fed females were kept together for one week, when the males were removed; these females averaged 242 eggs each during a 13-week period following exposure to the males, with maximum average production of 133 eggs for a 28-day period during the third to sixth weeks; 91.9% of these eggs hatched. Egg production declined sharply after eight weeks and virtually stopped by the 13th week, but when males were then added to the colony production increased to 0.9 egg per day per female. When starvation was imposed on a well-fed colony active in egg production, this production declined 92% between the fourth and seventh days, and only one egg was laid after the first week of starvation.

In 1925 List proposed the name *Hesperocimex* for the then monotypic genus based on the new species *Hesperocimex coloradensis* List, 1925. This species was described from a total of eight specimens; the holotype female was collected at Colorado Springs, Colorado, February 16, 1916, by W. D. Edmonston; the allotype male and five paratypes were also collected at Colorado Springs, Colorado, by the same collector on March 13, 1916. No host was given for the holotype; the allotype and five paratypes were reported as infesting a house with no other information being given as to whether this dwelling had previously been used by Purple Martins. The eighth and last specimen in the series before List at the time *Hesperocimex coloradensis* was described was a paratype from "Mexico" collected in the nest of a Purple Martin.

A previously unreported collection of *Hesperocimex* has been made available to the writer through the kindness of Jean M. Linsdale and Donald D. Linsdale. These specimens were taken from a nest of *Progne subis subis* Linnaeus, 1758, at Cachagua Creek in Monterey County, California, December 4, 1955. The history of this collection is of interest: the tree in which the Purple Martin's nest was located was blown to the ground and subsequently occupied by chipmunks, *Eutamias* sp.; the cimicid collection was made by mammalogists while they were searching the chipmunk's nest for ectoparasites. The chipmunk of course had appropriated the abandoned Purple Martin's nest after the nest-tree had fallen to the ground. These specimens of cimicids are morphologically similar to, and at this time indistinguishable from, the Colorado population of *Hesperocimex coloradensis*. If at all possible crosses should be made between the California population and the Colorado population of *Hesperocimex* to determine if the two populations are genetically inter-fertile. Such a study should confirm or invalidate the present concept which is based on morphological grounds.

To date, all attempts to secure live specimens of the genus *Hesperocimex* from east of the Rocky Mountains have been unsuccessful. Nest material examined from Blue Island, Illinois; Two Rivers, Wisconsin; and Darlington, Wisconsin, contained no cimicids or evidence that these ectoparasites had been present. The usual arthropod inhabitants of the several nests examined were fleas, mites, dermestids, and scenopinid larvae. Nest material collected by A. F. Wicke during July, 1956, in Pensacola, Florida, contained live adults and nymphs of *Cimexopsis nyctalis* List; a second

[1]Accepted for publication June 3, 1957. Since this paper was submitted for publication, the author has had the opportunity to collect cimicids which are morphologically similar to *Hesperocimex sonorensis* from the following localities: 28 mi. S. Punta Prieta, Baja California (North); 29 mi. S. El Arco and 9 mi. N.E. San Ignacio, Baja California (South); 9 mi. S. Kelvin, Pinal Co., Arizona; 15 mi. N.E. Imuris, Sonora, Mexico. The above specimens were collected by R. E. Ryckman, A. E. Ryckman, J. V. Ryckman, R. K. Ryckman, and Dean Spencer.

At this writing (December 15, 1957), crosses are being made between the type colony of *H. sonorensis* and members of the several colonies mentioned above. The results of these crosses, ecological information, and additional host records will appear in a subsequent paper.

collection on January 21, 1957, contained 23 adults. This is the first report of this cimicid from a host other than the Chimney Swift.

In California the Purple Martin does not nest in bird houses but rather in woodpecker holes in the tops of tall, dead trees, usually located in isolated forest areas which have been burned over. During the summer of 1956 the writer observed nesting Purple Martins north of Alpine Lake, Marin Co. Three nesting pairs were observed on July 5 in the tops of tall, dead fir trees in an area burned over approximately ten years previously. On July 22, 1956, a pair of Purple Martins were observed nesting in a tall, dead snag near the China Road on the north side of Big Basin Redwoods State Park, Santa Cruz Co. At this date the young birds were sitting on dead branches near the nest cavity. On July 19, 1956, a nesting site was studied in Hecker Pass, west of Watsonville, Santa Cruz Co. One or more pairs of adults had nested in the top of an extremely tall, dead redwood tree. On the date mentioned above several young birds were making short flights from branches near the several woodpecker holes present. Nest material has not been obtained from these nests to date because of the difficulty and hazard involved in climbing or felling these extremely large dead trees. Information concerning the nesting period is presented because of the importance this factor may have on the duration of starvation which the cimicids must withstand.

From 1925 until the present, the writer knows of only one published report (Lee and Ryckman, 1955) which is concerned with the collection of additional specimens which could be assigned to the genus *Hesperocimex*. Lee and Ryckman (1955) have reported *Hesperocimex coloradensis* from 18 miles southeast of Guaymas, Sonora, Mexico; this collection was made on August 24, 1954, by R. E. Ryckman, C. P. Christianson, and D. Spencer. The host *Progne subis hesperia* Brewster, 1889, was nesting in an abandoned wookpecker hole approximately 15 feet above the ground in *Pachycereus pecten-aboriginum*(Engelm, 1886), a saguaro-like cactus. At the time the collection was made the young birds were well feathered and capable of limited flight; the population of Purple Martin bugs had built up to an estimated number of several hundred. A sizeable live colony was collected and reared in the School of Tropical and Preventive Medicine, Loma Linda, California.

It has recently been possible for the writer to compare specimens taken from the colony established from the locality mentioned above with the allotype male and a paratype female of *Hesperocimex coloradensis* List. A study based on morphological characters indicates that the cimicid population collected near Guaymas, Sonora, Mexico, is quite distinct from the population described by List under the name *Hesperocimex coloradensis*.

The systematics and distribution of the host species may eventually be of assistance in determining the distribution and extent of speciation in the genus *Hesperocimex*. Ornithologists now agree that it is impossible to distinguish between an eastern and a western population of *Progne subis subis*; the former concept of an eastern and a western race or subspecies of this Purple Martin can no longer be defended. However, those Purple Martins breeding in the cacti of Sonora, Mexico, can be distinguished from the population of Purple Martins inhabiting eastern and western United States exclusive of the saguaro cactus belt of Arizona. *Progne subis subis* nests in tree holes and comparatively recently in domestic shelters in eastern United States. It is of significance to note that *Hesperocimex* from Colorado and California appear to be all of one species while the population of *Hesperocimex* parasitizing *Progne subis hesperia* from Sonora, Mexico, appears to be distinct from the Colorado and California populations in the United States. This would seem to indicate a geographical host-parasite relationship which has permitted cimicid speciation to occur in the two separate subspecies of *Progne subis*.

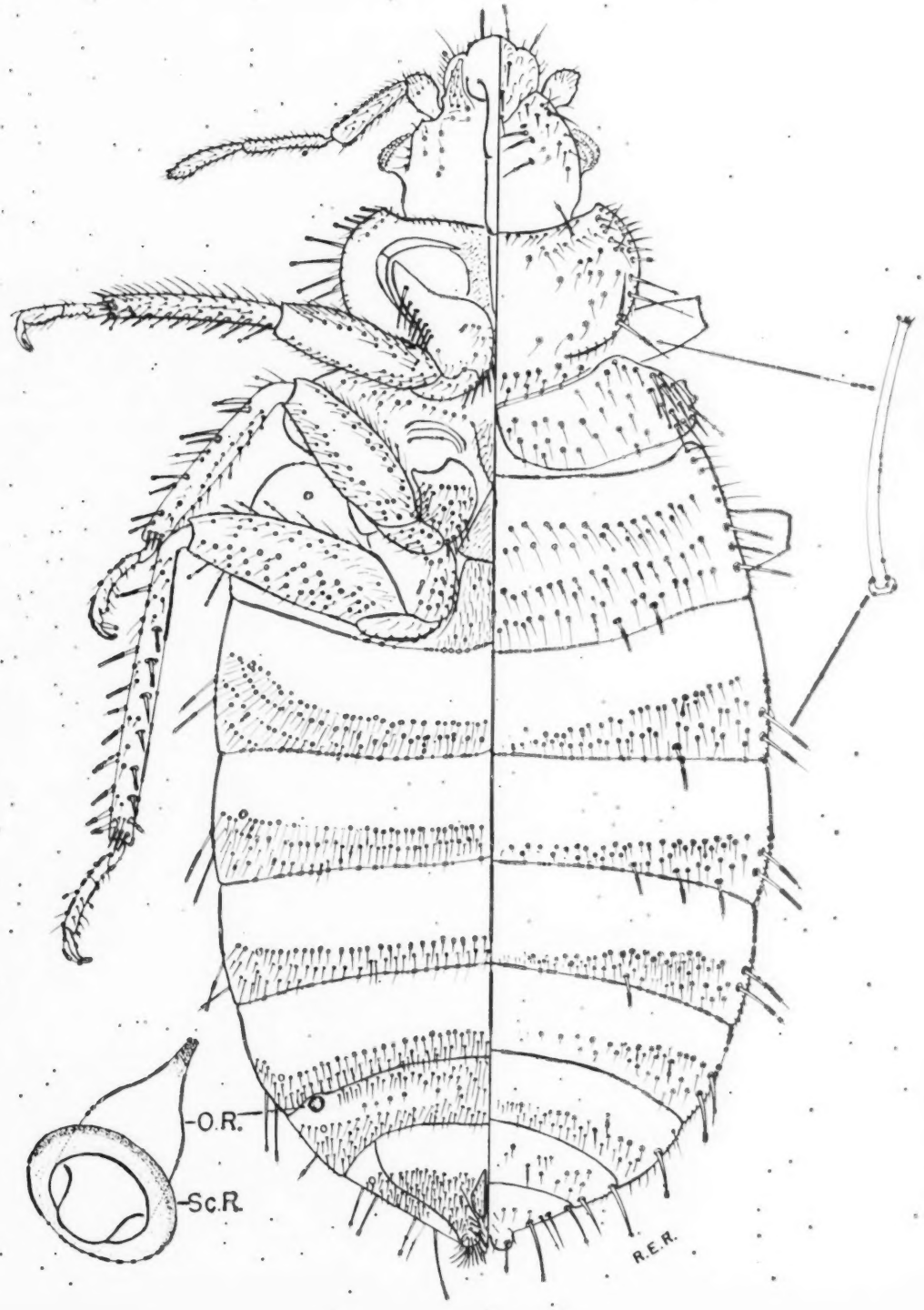
Hesperocimex sonorensis Ryckman, new species

The specific name *sonorensis* has been proposed for a population of cimicids parasitizing the Purple Martin, *Progne subis hesperia* in the state of Sonora, Mexico. It is believed that this parasite is endemic to the saguaro cactus belt of Sonora, Mexico, and southern Arizona of the Unites States.

Holotype female: General body color dark brown above, light brown on ventral surfaces, legs amber brown. Labrum, clypeus and anterior portion of head to margin of eye sparsely clothed with long bristles. Head broad, length shorter than width, 0.65:0.75 millimeters; interocular space 0.54 mm. Eye diameter 0.16 mm. by 0.09 mm. depth. Rostral segments subequal, third or terminal segment, longest, 0.26:0.24:0.29 mm. total length 0.79 mm.; tip of rostrum reaching to posterior margin of first coxal cavity. Antennal segments sparsely clothed with bristles, second

EXPLANATION OF FIGURES

FIG. 1.—Dorso-ventral view of the holotype female of *Hesperocimex sonorensis*. The enlarged figure of the Organ of Ribaga is a stylized, composite drawing indicating the gross morphology of this structure. Sc.R.—is a sclerotized ring connecting the (O.R.) Organ of Ribaga proper with the integument of the sixth apparent abdominal segment. The funnel-shaped portion of the structure is internal, and projecting into the abdominal cavity. The small prominence in the center of the sclerotized ring is that part into which the external male intromittent organ is inserted. No actual orifice was ever seen in the external portion of the Organ of Ribaga. A comprehensive conception of the Organ of Ribaga was made possible by specialized clearing techniques of whole mounts using methyl salicylate and beechwood creosote.


O.R.
Sc.R.
R.E.R.

segment longest, twice length of first segment; antennal segment ratios 0.17:0.34:0.30:0.26.

Thorax possessing many long stout bristles on pronotal expansion and on outer margin of hemelytral pads; length of outer, lateral margins of pads 0.37 mm. Pronotal expansion well developed, pronotum over twice as broad as long, 1.06:0.45 mm. Mesothoracic notum on medio-posterior region with only a slight indication of scutellar process. Coxae not contiguous, coxae of second and third legs more widely separated than coxae of fore legs. Mesosternum, metasternum, and venter of first abdominal segment forming a prominent keel separating the second and third pairs of coxae. Mesosternal keel ending anteriorly just before posterior margin of prosternum; metasternum broadly triangular. Ostiolar peritreme or scent gland opening located on ventral aspect of metathoracic subcoxae with long slender stem-like process extending medially. Scent gland approximating shape of Australian boomerang with outer portion of angle pointing anteriorly and second or stem-like portion of angle directed medially to base of subcoxae. Legs moderately long, well developed, first and second pair essentially equal in length, third pair longer than first or second pair of legs. First pair of legs—femur and tibia of equal length; coxae length nearly twice width, 0.45:0.23 mm.; trochanter length, 0.28 mm., width, 0.09 mm.; femur length, 0.58 mm., width, 0.17 mm.; tibia length, 0.58 mm., width, 0.075 mm.; tarsal segments 1–3, ratios of length to width, 0.083:0.033 mm., 0.091:0.033 mm., 0.166:0.041 mm., third tarsal segment twice length of first; two claws, length, 0.099 mm. Second pair of legs—tibia longer than femur; coxae length to width, 0.41:0.32 mm.; trochanter length, 0.29, width, 0.09 mm.; femur length, 0.66 mm., width, 0.24 mm.; tibia length, 0.75 mm., width, 0.08 mm.; tarsal segments, 1–3, ratios of length to width, 0.083:.033 mm., 0.116:0.041 mm., 0.174:0.049 mm.; two claws, length 0.108 mm. Third pair of legs—tibia obviously longer than femur; coxae length, 0.39 mm., width 0.33 mm.; trochanter length, 0.29 mm., width, 0.099 mm.; femur length, 0.79 mm., width, 0.25 mm.; tibia length, 1.05 mm., width, 0.09 mm.; tarsal segments 1–3, ratios of length to width, 0.099:0.041 mm., 0.124:0.049 mm., 0.215:0.049 mm.; two claws, length, 0.116 mm. Comparing first, second, and third pairs of legs, all limb segments except coxae show relative increase in length from anterior to posterior segments. Ratio of femur lengths on legs 1–3,0.58:0.66:0.79 mm., ratio of tibia lengths on legs 1–3, 0.58:0.75:1.05 mm.

Abdomen width, 2.5 times width of head including eyes. Posterior margins of abdominal sclerites, dorsum and venter, clothed with small to medium length setae; dorsum of first apparent abdominal segment sparsely covered with setae throughout; lateral margin of first apparent abdominal segment with four to five long bristles; abdominal segments, two to eight with one or more, often two, long bristles on lateral margins.

Organ of Ribaga located on right anterior margin of venter of sixth apparent abdominal segment. Sclerotized portion of organ of Ribaga (cleared specimen), 0.124 mm. width by 0.124 mm. in depth; organ appears set in circular plate less densely sclerotized than organ of Ribaga. A small tubular structure extends from organ of Ribaga into abdominal cavity. An enlarged drawing of the organ of Ribaga, and the holotype female, is illustrated in figure 1.

Holotype, female, from 18 miles southeast of Guaymas, Sonora, Mexico, August 24, 1954, R. E. Ryckman, C. P. Christianson, D. Spencer; host *Progne subis hesperia*.

Allotype, male, similar to holotype in all respects mentioned above except for well developed tibial brushes on inner distal aspect of first and second pairs of legs, and the genital capsule. Male genitalia, total length of sclerotized portion in cleared specimen, 0.356 mm. External portion of sclerotized intromittent organ essentially straight with decided curve or bend near tip; curved portion, 0.075 mm. in length. The genitalia of the allotype male are illustrated in figure 2.

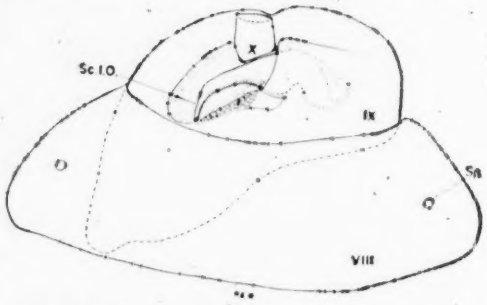


FIG. 2.—Ventral view of the posterior abdomen of the allotype male of *Hesperocimex sonorensis*. Sc.I.O. is the sclerotized portion of the intromittent organ. That portion of the genitalia expressed by dotted lines is internal. The curved tip at the distal end of the intromittent organ is the cardinal character separating *Hesperocimex sonorensis* from *Hesperocimex coloradensis*. Sp.—spiracle; VIII, IX, and X are body segments.

The holotype female and allotype male have been placed in the U. S. National Museum, Washington, D. C. Fifty-six paratypes have been designated; these specimens have been placed in the U. S. National Museum, Washington, D. C.; British Museum of Natural History, London, England; California Insect Survey Collection, University of California, Berkeley, California; California Academy of Sciences, San Francisco, California; and the Section of Entomology, School of Tropical and Preventive Medicine, College of Medical Evangelists, Loma

Linda, California. The holotype, allotype, and paratypes were all obtained from a single interbreeding colony originating from one nest of Purple Martins, *Progne subis hesperia*.

Immature Stages.—The relative sizes of morphological characters can best be understood by consulting table 1. A study of this table will reveal that the head is wider than long in all instars; in instars one to three the fourth antennal segment is the longest; in instars four to five the second antennal segment becomes the longest segment. The third segment of the rostrum is equal to or longer than segments one or two in all instars; the first segment equals or is longer than the second segment in all immature instars. females are not present in the immature stages; however, the dorsal abdominal scent glands are present in all immature stages. In the last or fifth instar nymphs there is no apparent external indication of the organ of Ribaga in female nymphs or external male genitalia in the male nymphs.

The eggs of *Hesperocimex sonorensis* are white, semiglossy and oblong in form, measuring 0.98 mm. in length by 0.48 mm. in width. A circular cap or operculum is situated on the anterior, upper surface of the egg. Opercula removed from the eggs after hatching measured 0.259 mm. in diameter. The eggs are very effectively glued to the blotter paper in rearing vials or to

TABLE I

Table of Mean Measurements of Immature Stages

	Head			Pronotum		Antennal Segments				Rostrum		
Instar	Length	Width	Interocular	Length	Width	1st	2nd	3rd	4th	1st	2nd	3rd
1st	0.27	0.36	0.24	0.13	0.47	0.07	0.11	0.12	0.14	0.12	0.12	0.17
2nd	0.33	0.42	0.30	0.2	0.54	0.09	0.14	0.13	0.17	0.17	0.14	0.17
3rd	0.38	0.49	0.35	0.24	0.64	0.12	0.17	0.17	0.21	0.21	0.17	0.21
4th	0.53	0.69	0.45	0.35	0.82	0.14	0.24	0.20	0.22	0.22	0.18	0.24
5th	0.64	0.7	0.49	0.39	1.0	0.17	0.32	0.26	0.25	0.26	0.21	0.29

TABLE II

Diagnostic Comparison of *Hesperocimex sonorensis* and *coloradensis*

Species	Head Length	Pronotum Width	Color	Male Genitalia
H. sonorensis	0.65 mm.	1.06 mm.	Dark brown above.	Terminal portion of external genitalia strongly curved.
H. coloradensis	0.74 mm.	1.30 mm.	Yellowish brown above.	All of external genital structure straight.

The pronotum increases in width at a relatively more rapid rate than length in the fourth and fifth instars. The hemelytra are present in all immature stages but are quite small in instars one to three. Immature stages have only two tarsal segments, whereas adults have three tarsal segments.

Between individuals of a given instar there is obviously some variation in size of the morphological structures measured. Data presented in the above table were drawn from 21 immature nymphs; however, in no case was the maximum measurement for a younger instar greater than a given measurement of the next older instar.

The tibial brushes, located on the inner distal aspect of the first and second tibiae in adult males, are not present in the immature stages. Likewise the thoracic ostiolar peritremes, or scent gland openings, present in adult males and smooth glass surfaces. If an egg is laid in such a way that it is in contact with two pieces of paper at one time or a piece of paper and the glass wall of the shell vial, the glue-covered egg will effectively hold the two surfaces together; two pieces of blotter paper thus joined together may be picked up and gently waved through the air without breaking apart. Eye spots appear in the developing eggs by the end of the third day.

Diagnostic Description.—*Hesperocimex sonorensis* may be distinguished from *Hesperocimex coloradensis* by the table of comparative characters which are summarized in table 2.

Curatorial Techniques.—Immature and mature specimens were prepared for study by clearing in beechwood creosote or depigmenting in ten per cent sodium hydroxide or both; after being cleared and depigmented, the specimens were transferred through ethyl alcohol to xylol and

mounted in Canada balsam. The internal abdominal organs were dissected out of the abdominal cavity during or after the clearing and depigmenting process. Some of the best specimens of the organ of Ribaga were prepared in beechwood creosote and in methyl salicylate.

The first pair of coxae may occasionally appear to be contiguous in mature and immature specimens mounted on slides if the pressure of the cover slip is too great or if the legs have been changed from their natural position. The coxae of *Hesperocimex sonorensis* are not contiguous in live specimens or those preserved in alcohol.

Measurements.—All measurements given in the descriptions mentioned above have been obtained with the aid of a calibrated ocular micrometer. The ratios have been given in actual millimeters which not only makes available the ratio of one structure to another structure but also the actual size of the structures in millimeters.

The length of the abdomen was not included in the measurements because the abdominal length is highly variable in both males and females depending on the nutritional condition of the individual.

BIOLOGY

The breeding colony was secured from live material collected 18 miles southeast of Guaymas, Sonora, Mexico. All of the bugs used in the life-history studies were reared in an incubator under uniform conditions of 80° F., or 27° C., plus or minus two degrees F. and a relative humidity of 75 per cent plus or minus five per cent.

Material and Methods.—The laboratory host for the cimicid colonies throughout this experiment was a White Leghorn hen; the host was restrained while the bugs were being fed in a manner similar to that described by Lee (1955).

Stock colonies of the bedbugs were maintained in shell vials measuring 40 mm. x 95 mm. Experimental colonies were reared in shell vials 25 mm. x 95 mm. Fifth instars individually isolated to obtain virgin males and females were held in small shell vials 8 mm. x 90 mm. These vials were thoroughly washed with green soap and rinsed after the first experiment; in the initial study nearly 100 first instar-nymphs were individually isolated in new, unused shell vials as they came from the manufacturer. Most of these nymphs died. In subsequent studies when all the vials were washed and rinsed, a very low mortality or no mortality at all occurred.

All of the experimental vials were covered with a fine mesh nylon hose which was held in place by rubber bands stretched tightly around the lip of the shell vials. Green blotter paper was used as a convenient substratum for the bugs. This paper has the advantage of quickly absorbing the fecal droppings and furnishing a readily acceptable surface on which the females may oviposte (Ryckman, 1952). The blotter was used in two ways, either folded in accordion-like folds and inserted into the vials, or two small slightly curved cards of blotter paper were inserted in each rearing vial to furnish crevices for the bugs to hide in and for them to oviposit on. Best results were obtained when the cards of blotter paper were not more than three centimeters in length; at feeding time this technique brought the bugs down close to the host and made possible more rapid and uniform feeding. Colonies being studied for oviposition were supplied with small cards of blotter paper slightly smaller than the inside diameter of the vials. It was found that if lines were scribed on the blotter paper with a blunt instrument the bugs would lay their eggs in these small grooves; this method greatly facilitated the counting of the eggs. When the lines were not provided the bugs frequently laid as many as 50 to 75 eggs in a mass which made counting rather difficult.

A binocular microscope was used when eggs were counted, when mortality checks were made, or when other statistical data were taken; this was done to assure accuracy and to permit a more precise record of the behavioristic phenomenon, such as copulation behavior, occurring in the shell vials.

Number of Pre-adult Instars.—Lee (1955) found that *Haematosiphon inodorus* had only four immature instars. Since *Hesperocimex* and *Haematosiphon* both belong to the same subfamily it was thought that for phylogenetic reasons the number of immature instars in *Hesperocimex* should also be studied. A series of 109 eggs were individually isolated in small shell vials; when the eggs hatched the nymphs were retained in the shell vials and permitted to feed through the nylon cover as mentioned above. At each instar a number of nymphs was preserved in ethyl alcohol with their cast skins. At the conclusion of this study all adults, males and females, were found to have passed through five pre-adult instars. The nymphs with correlated cast skins were mounted on slides for study. With respect to number of pre-adult instars, there does not seem to be phylogenetic correlation between *Hesperocimex sonorensis* and *Haematosiphon inodorus*.

Table 3 indicates the mean developmental time in days required for each instar and the incubation period for the eggs at 75 percent relative humidity and 80° F.

Starvation Studies.—It is rather obvious that the Purple Martin hosts are not present at the nesting site for long periods of time after the young birds have been reared (Allen and Nice, 1952). It is therefore of importance to know how long the adults and immatures may be expected to live without food. Myers (1928) working with *Oeciacus vicarius*, found that the swallow bug was capable of living for six months without food and gave further evidence to indicate that the bugs were able to over-winter in the

old nests until the return of the hosts the following spring. The writer collected 133 live specimens of *Oeciacus vicarius* from four old Cliff Swallow nests on the campus of the University of California at Berkeley during late winter: i.e. March 19, 1957. This collection consisted of 77 nymphs in instars two to five, 22 females and 34 males; none of the specimens had fed for a considerable period of time. This collection was made a short while before the expected return of the Cliff Swallows to determine the instars and total number of bugs which had over-wintered. Mr. A. F. Wicke kindly collected, for the writer, 23 live adult males and females of *Cimexopsis nyctalis* from a Purple Martin house in Pensacola, Florida, on January 27, 1957. He reported that the Martin house did not appear to have been occupied for a considerable period of time but that this house had been occupied by Purple Martins and Starlings the previous summer.

TABLE 3

MEAN DEVELOPMENTAL PERIOD FOR EGGS AND IMMATURE STAGES

STADIA	MEAN DEVELOPMENTAL PERIOD
Egg	6 days. None hatched on fifth day. All hatched before seventh day.
1st Instar.	8.1 days. Maximum 11 days; minimum 7 days.
2nd Instar.	7.06 days. Maximum 11 days; minimum 5 days.
3rd Instar.	5.4 days. Maximum 7 days; minimum 5 days.
4th Instar.	5.5 days. Maximum 7 days; minimum 4 days.
5th Instar.	8 days. Maximum 9 days; minimum 7 days.
1st Instar-Adult.	Males, 33.3 days; females, 36 days.
Egg-Adult.	Males, 39.3 days; females, 42 days.

Sooter, Bennington, and Daniels (1954) have shown that many species of birds other than Swallows may frequent unused Swallow nests for brief or extended periods; this is especially true during the fall and winter seasons when adverse climatic conditions induce birds to find shelter. It is quite probable that under such conditions some of the cimicids would find it possible to break their compulsory fast and take a blood meal which should then extend their survival period for some time. Sooter, Bennington, and Daniels (1954), working in Colorado, have reported the English Sparrow, *Passer domesticus* (Linnaeus, 1758) and Say's Phoebe, *Sayornis saya saya* (Bonaparte, 1825) nesting in abandoned nests of the Cliff Swallow, *Petrochelidon pyrrhonota pyrrhonota* (Viellot, 1817). These workers also reported that three Finches frequented the Cliff Swallow nests during the wintertime over a ten-year period of observation. The Finches reported in this investigation were the Rosy Finch, *Leucosticte tephrocotis littoralis* Baird, 1869; *L. tephrocotis tephrocotis* (Swainson, 1831); and the Black Rosy Finch, *L. atrata* Ridgway, 1874. The Canyon Wren, *Catherpes mexicanus conspersus* Ridgway, 1873, was also found associated with the Cliff Swallows. Pitelka (1944) reported the White-throated Swift, *Aeronautes saxatalis* (Woodhouse, 1853) nesting in a Cliff Swallow nest with a colony of Cliff Swallows on the University of California campus at Berkeley, California. From the above it would seem that it is not uncommon for birds to use or in some way associate themselves with the nests of other birds. It is quite possible that the fall and winter visitations of birds seeking shelter in the nests and nesting cavities used by other birds could be an important factor in the survival of many ectoparasites including *Hesperocimex*. In order to determine the effect of starvation on mature and immature stages of *H. sonorensis*, the following five studies were conducted.

Twenty-nine first instar nymphs were permitted to feed but once and were then starved; 14 of these nymphs molted to the second instar; these second instars did not live beyond the 37th day after their first blood meal. Thirty-nine first instar nymphs were permitted to feed twice on successive days; 34 of these nymphs molted to the second instar. None of these second instars lived beyond the 56th day after the last blood meal. In a third colony 100 first instar nymphs were permitted to feed on three successive days; many of the nymphs did not feed when given the opportunity to do so on the third day. Ninety-nine of these nymphs molted to the second instar; all of the second instars lived for 17 days, and the last nymph died on the 63rd day subsequent to the last blood meal.

From the above it is apparent that two to three blood meals are adequate to enable a first instar nymph to molt to a second instar nymph; it is also quite evident that these bugs will feed more than once in the first instar.

A single female which emerged as an adult on March 26, was permitted to mate once but was never fed at any time during her adult life. She lived until June 20 and died at an age of 86 days. This female laid two unfertile eggs when seven days of age. Four females which had not received a blood meal as adults were exposed to three males for 48 hours soon after the females emerged; these females laid a total of 12 fertile eggs by the time they were seven days of age. One female died when 29 days of age, a second female died at age 53 days, and the remaining two females were dead by the 63rd day. The number of eggs laid and fertilization data are given because it is believed that the number of eggs laid by a female will have a direct relationship to her potential length of life under starvation conditions. This is inferred to apply to those females which have never had a blood meal

in the adult stage. In a fourth starvation test two unfed males and one female were confined together in a shell vial and were observed periodically until they died; the female laid two fertile eggs and died at the age of 69 days; the males died at 69 days and 77 days. In a fourth starvation study nine unfed virgin females were mated with 20 fed, virgin males; these females laid 13 fertile eggs and lived as adults from 53 days to 73 days. The 20 fed males mentioned above were permitted to feed to repletion three times before being exposed to the females; the males were two to ten days of age when given an opportunity to feed. Six of the 20 fed males were dead by the 46th day after their last blood meal; the remaining males died at the following ages, respectively: 69th, 74th, 77th, 81st, 90th (2), 104th, 115th, 130th, 134th, 189th, and 208th day of starvation.

In a fifth starvation study 14 males and eight females were united together into one colony. The adults comprising this colony emerged as adults from March 6 to 16 and were fed five times per week until May 29; on this date, or when the bugs were approximately 70 days of age, all subsequent feedings were discontinued. This study is to simulate conditions in a Purple Martin's nest after the fledglings and adults have left the nest, theoretically forcing the cimicids to undergo conditions of starvation. On the 17th day of starvation the first dead bugs were seen in the colony; by the 21st day of starvation three of the eight females were dead and two of the 14 males were dead; by the 27th day of starvation a total of six of the eight females were dead and six of the 14 males were dead; by the 49th day seven of the eight females were dead and 11 of the 14 males; by the 59th day all of the males were dead and all but one of the eight females; the last female was dead by the 66th day. The females in this colony died at a relatively more rapid rate than the males in the initial portion of the starvation period, but the last adult to die was a female which had existed without a blood meal for over two months.

A sixth colony used in starvation studies consisted of 15 individually reared males and 15 females which were never fed in the adult. The females laid nine eggs, eight of which hatched. One male and one female died after 46 days of starvation in the adult; after 74 days of starvation five males were dead and 11 females were dead; after 99 days of starvation ten males and 12 females were dead; after 138 days of starvation 14 males and 13 females were dead; by the 155th day 14 males and females were dead, and the last male died by the 169th day and the last female by the 218th day.

Mating Behavior.—Virgin males which have emerged in individual vials appear to have a very strong sex drive when released with other males or females. When virgin males are brought together they readily climb on the backs of other males and assume a copulatory position. The male which has been mounted usually conducts a dance shortly after having been mounted and thereby dislodges the aggressive male from his back. This dance follows a very characteristic pattern wherein the male which has been mounted conducts a violent sidewise or transverse shaking motion which seems more to annoy the rider than to physically dislodge him. The transverse motion of the male is accomplished by a side to side rocking motion with the legs being used as the point of pivot. This dance is not unlike the tail-wagging dance of honeybees described by Von Frisch. When individually reared virgin females are brought together an occasional passive gesture to mount another female may occur, but in general there are few such attempts.

Virgin males introduced into a vial with virgin females, or with mated females, seem to be capable of recognizing a female only at a relatively short distance. It would seem that the male is approximately the length of his antennae from the female before he reacts in a definite manner. Once the female has been detected the male climbs upon her back with a very swift almost jumping motion. The female may remain relatively quiet throughout the entire period of copulation, or some females may dash about wildly in an apparent attempt to dislodge the male. In the latter situation the male clamps his first and second pairs of legs around the female's body in a vice-like grip from which she is unable to release herself. The male's legs are flexed at the femora-tibial joint, thus forming an acute angle which fits over the lateral margins of the female's thorax or the anterior abdominal segments if the female is engorged. Occasionally females have been observed engaging in the tail-wagging dance but even this violent motion is not adequate to dislodge the persistent males.

In the typical copulatory pattern the male quickly mounts the female and directs the terminal portion of his abdomen over the right side of the female's abdomen. (The organ of Ribaga is located ventrally near the right, lateral margin of the female's sixth abdominal sclerite.) The internal portion of the male genitalia is located in the right half of the ninth abdominal segment; the external portion or sclerotized intromittent organ, the gonostyli of Davis (1956) or the parameres of Singh-Pruthi (1925) and Dupuis (1955), lies in an open transverse groove in the left half of the same segment. There is a decided curve in the terminal portion of the intromittent organ; it is the tip of this curved portion of the aedeagus which probes about on the ventral surface of the female's abdomen near the organ of Ribaga (see figure 2). The male appears to be able to detect by some means when the tip of the intromittent organ has contacted the surface of

the organ of Ribaga. When the organ of Ribaga is located, more precise probing motions are conducted; usually with little further effort the male genitalia are inserted into the female's organ of Ribaga. The abdomen of the female is not pierced but rather the male genital structure is inserted into the specialized pouch, the organ of Ribaga. It was of interest to note that in slide mounted specimens the sclerotized portion of the organ of Ribaga was 0.15 mm. in depth and that the curved portion of the male's intromittent organ was 0.09 mm. in length. The male intromittent structure has been seen inserted into the organ of Ribaga to a depth slightly beyond the curve in the distal portion of the external portion of the male genitalia. Males will readily copulate with very young virgin females as observation on the following study will indicate. A female emerged in a vial containing fourteen males and nine females. Within less than fifteen minutes and while the female was still white (unpigmented) the males began to "ball" her; as many as four males were tenaciously trying to copulate with her at one time. On several occasions there were three males mounted on top of each other with the first male on the back of the female. During another study three virgin males were given an opportunity to copulate with five unfed virgin females, one of which had just emerged and was still white or unpigmented. The recently emerged and unpigmented female emerged at 10:04 A.M. and with the other four virgin females, which were from one to three days old, was exposed to three males at 10:12 A.M.; by 10:14 A.M. all three males were in physical copulation. The unpigmented female was the last of the three females covered by a male. The young unpigmented female was in actual physical copulation from 10:14 A.M. to 10:26 A.M., and a second pair ended copulation at 10:37 A.M. These pairs were in copulation for 12 and 23 minutes respectively. The male which had copulated with the young female remained on her back but not in copulation from 10:26 A.M. until 12:16 P.M.; thus the total period of contact between male and female was from 10:14 A.M. to 12:16 P.M., or two hours and two minutes.

Sex Ratio.—In excess of 300 last instar nymphs were removed from a continuously breeding colony to determine the sex ratio of males and females. The adults which emerged in this colony were removed and examined in three groups over an extended period of time. In each lot removed, the males were more numerous than the females. Since there were more males in the first and the last group removed, this would seem to indicate that the developmental time for both sexes is approximately equal; this concept is further supported by the data presented in the section entitled, "Number of Pre-adult Instars." The mean developmental period for males was 33.3 days and 36. days for females.

In the 301 individuals which reached the adult stage, 187 were males (62.12%) and 114 were females (37.87%). The males are capable of fertilizing females for the greater portion of their lives. Considering the above, it is not clear why this ratio of 1:1.64 females to males should occur.

FERTILITY AND FECUNDITY STUDIES

The following studies may be divided into five sections relative to the manner in which the experimental colonies have been handled, namely: I—Males and Females Fed, Normal Reproduction; II—Males and Females Not Fed, Autogenous Reproduction; III—Males Fed and Females Not Fed; IV—Females Fed and Males Not Fed; and V—Fed Virgin Females. The field reproductive potential of an insect species can not be well understood until certain factors are known concerning (1) the fertility and fecundity of the population concerned as affected by the availability and frequency with which food is required to maintain reproduction, (2) the potential of autogenous reproduction, and (3) the survival period or life expectancy of males and females.

I. Males and Females Fed, Normal Reproduction.—In this study two colonies were established containing males and females of known age and sex ratio. These colonies were given an opportunity to feed to repletion on five successive days of each week; a White Leghorn hen was used as the host. The colonies were confined in shell vials furnished with strips of blotter paper for the females to oviposite on. The cards of blotter paper upon which the eggs were laid were removed every seventh day, dated, and placed in individual shell vials. The eggs were then placed in the same incubator where the adults were reared, and the eggs were permitted to hatch. When all viable eggs had hatched the total number of eggs laid and the percent that had hatched were tabulated. There were a few eggs which were obviously fertile but from which no nymphs hatched. Some of these eggs did not hatch because the eggs were laid, on occasion, in such close proximity to each other that the emerging nymph was unable to push the operculum off the egg; however, most of the fertile eggs which did not hatch failed to do so for reasons other than those of a mechanical nature, such as that mentioned above.

Figure number 3 contains the fertility and fecundity data for Colony I. This colony was established with 23 adult bugs, 14 males and nine females which emerged to adults from March 5-15. Approximately two months after the colony had reached maximum production, all feeding was stopped to determine the effect of starvation on a previously well fed colony. This was done to simulate the condition existing in the Purple Martin nests after the fledglings have left the nest.

A study of figure 3 reveals that the females were producing 3.65 eggs per day per female during the second week after all of the females in the colony had emerged. A maximum of 4.98 eggs per female per day were laid by the colony during the tenth week of production; a mean of 3.36 eggs was laid per day per female during the first 11 weeks of reproductive activity. At the time the starvation test began the colony was laying eggs at the rate of 3.46 eggs per female per day. During the following four days of starvation the mean number of eggs laid per day per female dropped to 2.45, and during the following seven days egg production dropped to a low of 0.55 eggs per day per female. No eggs were laid after 11 days of starvation. From the above it is apparent that egg production declines rapidly and is completely terminated by the 11th day. During the first 11 weeks of reproductive activity the females laid 2,215 eggs; nymphs hatched from 96.20% of these eggs.

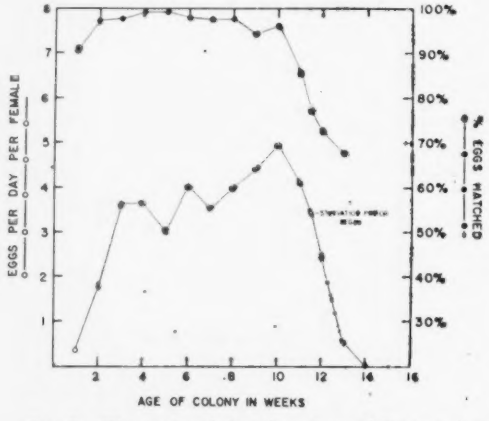


FIG. 3.—The productivity of a colony of *Hesperocimex sonorensis* consisting of 23 adults, fourteen males and nine females. During the first eleven weeks of reproductive activity, 2,215 eggs were produced. Approximately two months after the colony had reached maximum production, all feeding was stopped to determine the effect of starvation on a previously well fed colony.

Colony number two was established by 23 bugs, nine males and 14 females, which emerged as adults from March 12 to 23. This colony was maintained environmentally in a manner similar to that of Colony number 1 which is discussed above. The original purpose of this study was to determine how long a colony of *Hesperocimex sonorensis* may be expected to live under favorable conditions and the number of eggs and progeny produced per female per generation under optimum laboratory conditions. It is apparent after studying figure number 4 that the fertility-fecundity value for this species is quite high and that the females are capable of high and sustained egg production for a considerable period of time. Lee (1954), working with *Haematosiphon inodorus*, a member of the same subfamily to which *Hesperocimex sonorensis* belongs, found that the ovipositing females did not live beyond the 30th day.

Figure number 4 contains the fecundity data for this colony for a period of 46 weeks.

To determine if the reproductive decline during the 19th week was due to the males or females or both, the following experiments were conducted. The old males were removed and 16 males (under four months of age and not virgins) were added to the colony of 14 old females at the 19th week. During the 20–26th weeks a very limited number of eggs was produced, never more than 0.5 per female per day. A reciprocal of the above study was conducted wherein the seven old males which were still alive (two had died by this time) were exposed to a colony of six virgin females. These females produced a normal number of eggs with a high percentage fertile. It is therefore evident that the males were still capable of producing viable sperm when 20 weeks of age but that the females were no longer capable of laying more than a relatively very limited number of eggs. Since the cimicids possess telotrophic ovaries it would appear that when a predetermined number of oöcytes have been exhausted no more eggs can be produced regardless of how much longer the females may live. It is quite probable that in nature only a very few females live long enough, and under suitable environmental conditions, to be permitted to use the physiological maximum number of oöcytes produced.

This study was terminated after 46 weeks of investigation due to the fact that 12 of the 14 females had died and the surviving females had not laid during the last 18 weeks of this period. Furthermore, only one egg was laid during the last 21 weeks of the 46-week period mentioned above. It was therefore apparent that the physiological reproductive potential of this colony had been reached. A total of 5,195 eggs was laid by this colony of 14 females over a period of 28 consecutive weeks. This is equivalent to a mean of 371 eggs per female during their period of reproductive activity or a mean of 1.89 eggs per day per female during the entire period of 28 weeks. Since four of the females died during or before the 28th week, it is apparent that some females produced considerably more than 1.89 eggs per day per female during the period of 28 weeks. Nymphs hatched from 92.4% of the eggs laid, which in reality amounts to 343.14 viable first instars per female or 1.75 nymphs per female per day during the entire 28-week period. During the 7th to the 10th week inclusive, which was the four-week period of greatest activity, the 14 females laid 1,689 eggs or 120 eggs per female, which was a mean of 4.308 eggs per day per female during the entire 28-day period; there was a mean of 4.0 viable first instar nymphs pro-

duced per day per female during this peak period of 28 consecutive days.

II. Autogenous Reproduction.—This study was conducted to determine if unfed adult males and females were capable of producing living progeny without having had a blood meal after reaching the adult stage. A pilot experiment was conducted at first using two males and one female. The female laid two eggs, both of which hatched. The bugs mentioned above emerged as adults on March 26 and the two eggs were laid between March 30 and April 2, or when the female was from four to seven days of age. The female and one male were dead by the 69th day, and the remaining male was dead by the 77th day after reaching the adult stage.

A more detailed study was conducted using 15 unfed males and 15 unfed females. These bugs emerged as adults in individual rearing tubes from April 11–13 and were united into a colony of 30 members on April 16. The males were observed copulating with the females on April 19, but there is no reason to believe that they did not copulate with the females before this time. Six eggs were laid between April 20 and April 23. One additional egg was laid on each of three successive days, April 24, 25, and 26. This made a total of nine eggs laid by the 15 females. The first egg hatched on April 27, which indicates that this egg was laid on April 20 or 21. As previously indicated, the eggs usually hatch on the sixth to seventh day. By April 30 seven of the nine eggs had hatched, and by May 4 the eighth egg had hatched. Of the nine eggs laid, one was not fertile. From the above data it is evident that limited autogenous reproduction is possible. By May 18 all of the eight unfed nymphs were dead. On June 20 when the adult bugs were 70 to 72 days old a total of four of the 15 unfed males were dead, and eight of the 15 unfed females were dead.

III. Males Fed and Females Not Fed.—In these studies the males were well fed but the females were not fed. These experiments were conducted in an attempt to determine if there was any possibility of the females being nourished by excess sperm. The data obtained in these studies may be compared with the autogenous studies wherein the males and the females were not fed.

Four unfed virgin females which had emerged from March 23 to 26 were united with three well nourished virgin males on March 26; the nourished males had emerged on March 8, 14, and 18. These bugs were left together for 48 hours and then separated on March 28. Between March 30 and April 2 the four females laid 12 eggs; these eggs were laid from the fourth to seventh day after the unfed females had physical contact with males. All of the 12 eggs laid were fertile and produced twelve normal appearing nymphs. The males were fed after separation from the females on March 28 and then were reintroduced into the vial containing the females on April 12; no eggs resulted from this last union. The first unfed female died on April 24 at an age of from 32 to 35 days; between May 11 and 18 a second female died at an approximate

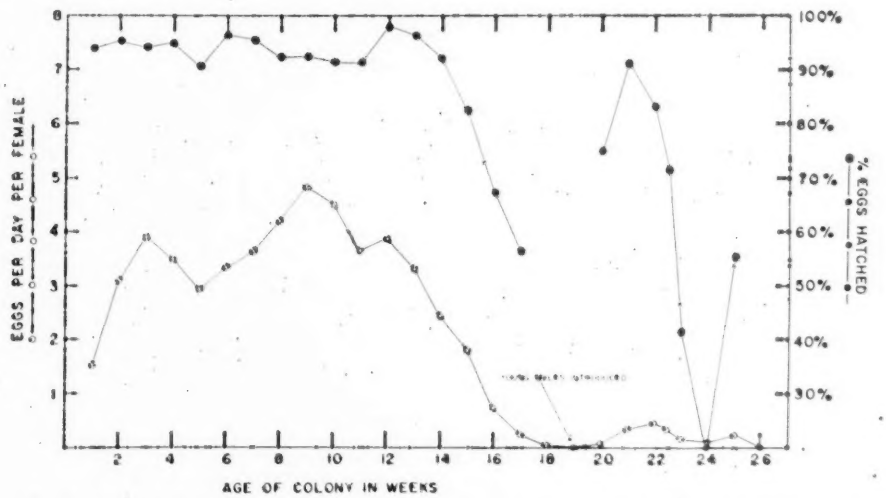


FIG. 4.—The productivity of a colony of *Hesperocimex sonorensis* consisting of 23 adults, nine males and fourteen females. A total of 5,195 eggs were laid by this colony of fourteen females over a period of 28 consecutive weeks.

The old males were removed and 16 males, all under four months of age, were added to the colony of 14 old females at the 19th week.

age of from 50 to 56 days; the last two unfed females were both dead by May 28 at an age of approximately two months.

In the strictly autogenic studies 15 females laid at the rate of six-tenths of an egg per female; in the study wherein the males were fed, four females laid three eggs per female.

A more detailed study using a larger number of unfed females and fed males was initiated to determine if the increased egg production obtained from the above colony could be repeated; i.e. would further investigation using larger numbers continue to indicate that unfed females mated to fed males were capable of producing more eggs than unfed females mated to unfed males.

On April 12, 20 young virgin males, which had previously been given the opportunity to feed to repletion on three occasions, were released into a vial containing nine unfed virgin females which were from one to ten days of age. Minutes after the males were introduced there were several copulating pairs present. Seven eggs were laid between April 13 and 16, and six eggs were laid on April 17. A total of 13 fertile eggs was laid by the nine females; this is a mean of 1.6 eggs per female. Combining the data from the two colonies it was found that 13 unfed females laid a total of 25 eggs, or a mean of 1.92 eggs per female as compared with 0.6 egg per female laid by a colony of 15 unfed females mated to fifteen unfed males. From these data it was found that unfed females mated to fed males laid more than three times as many eggs as the unfed females mated to unfed males. Since none of these bugs or any cimicids known to the writer have been reported engaging in coprophagous feeding or kleptohemodeipnonism (Ryckman, 1951) one might conclude that the difference in egg production between the two groups of females was in some way related to the condition of nourishment of the male and the amount of sperms produced. This view, however, should be considered with care since on one occasion as mentioned above, one unfed female mated with two unfed males produced two eggs.

A third experiment was conducted wherein there were four fed males per each unfed female. This experiment was conducted to determine the possible effects of an increased amount of sperm made available by increasing the ratio of fed males to unfed females. Six unfed, individually reared females which emerged on April 16 to 18 were mated with 24 fed, virgin males on April 18; the males had emerged April 11 to 13 and were given an opportunity to feed to repletion on April 16, 17, and 18. These six females laid four eggs from April 20 to 23, two eggs on April 24, one egg on April 25, and two eggs on April 27. This is a total of nine eggs laid by six females in seven days, or a mean of 1.5 eggs per female; all of the eggs laid were fertile. In this experiment what would appear to be an exessive amount of sperm available to the females did not result in a rise in egg production above the mean of 1.92 eggs laid by the unfed females which were mated with fed males involving a sex ratio of 13 unfed females to 23 fed males; this is less than two males per female; whereas in the last investigation reported above there were four fed males per unfed female. The addition of males up to four per unfed female failed to increase egg production, which would seem to indicate that the females are not very extensively if at all nourished by the sperm. Subsequent sections of this paper will reveal that fed or unfed females must copulate with the males before they are capable of laying any eggs; this of course is not implied necessarily to have any correlation with nutrition by sperm.

IV. Females Fed, Males Not Fed.—The fourth class of fertility-fecundity studies is concerned with the situation wherein the females are well nourished and the males are unfed. This study was conducted to determine if unfed males were capable of inseminating the females with a relatively large quantity of viable sperms. A second consideration was concerned with the period of time the females would be capable of laying viable eggs after separation from the males: i.e. are females capable of receiving and storing with one or a few copulations enough sperm to last for the rest of their natural lives.

On April 20, 28 individually reared and unfed males were united with 14 females which had previously been fed on April 17, 18, and 19. The males had emerged from April 11 to 16, and the females had emerged from April 11 to 13. Matings were observed within five minutes after the males and females were united into one colony. On April 23, or three days after the males and females were united, 14 eggs were present, and by the fourth day a total of 67 eggs were present. The males were permanently removed from the females after seven days. Figure number 5 indicates the rapid increase in egg production and the large number of fertile eggs this colony of fed females was capable of producing after having been exposed to unfed males for seven days.

This colony of 14 fed females laid a total of 3,396 eggs during a period of 13 weeks after exposure to 28 unfed males. A mean of 242 eggs was laid per female as a result of the initial seven days exposure to males; this would seem to indicate that this species of cimicid is capable of storing a large number of sperm, or at least of retaining viable sperm in their bodies, for a period upward to 13 weeks and of maintaining relatively normal reproduction as long as ten weeks after exposure to males. Maximum reproduction for a period of 28 consecutive days was attained during the third to sixth weeks inclusive, during which time 133 eggs were laid per female, or 4.75 eggs per day per female for 28 consecutive days. Nymphs emerged from 91.93% of the total eggs laid; this percentage compares rather closely with colony one in which nymphs hatched

from 96.20% of the eggs laid during an 11-week period and during which time the females were continuously exposed to males. Colony two, composed of 14 females continuously exposed to males, laid 5,195 eggs during a period of 28 weeks. Viable nymphs hatched from 92.47% of these eggs. These data would seem to indicate that essentially as large a percentage of viable nymphs will hatch from eggs laid by females fertilized only during a relatively short period of time early in their adult life as from those females which are continuously exposed to males. However, after a period of eight weeks there was a sharp decline in egg production in those females not continuously exposed to males, whereas this decline in egg production did not occur until the 14th week in colony two where females were in constant exposure to males.

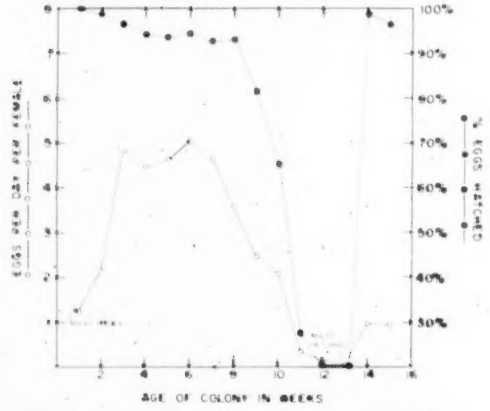


FIG. 5.—The productivity of a colony of *Hesperocimex sonorensis* consisting of 28 males and 14 females. The well fed virgin females were exposed to the unfed, virgin males only during the first seven days of this study; the females laid a total of 3,386 eggs during the 13-week period following exposure to the males. On the 13th week 16 virgin and well fed males were introduced into the colony of females to determine if this decline in egg production was due to an inadequate supply of sperm. This study was terminated on the 15th week.

To determine if the availability of sperm was a factor in the decline in egg production at the tenth week post-exposure to males, the colony was observed for the next three weeks, by which time egg production had essentially stopped: i.e. 0.02 eggs per day per female during the 13th week. At this point in the history of the colony 16 virgin males were added to the colony; during the subsequent week after exposure to the males the 14 females laid 95 eggs, or 0.97 eggs per day per female. This immediate rise in egg production is an indication that the absence of sperm was a limiting factor with respect to egg production.

V. *Nourished Virgin Females.*—The following studies were conducted to determine if well nourished unmated virgin females were capable of laying eggs.

Three individually reared virgin females which emerged to adults on March 12 and 18 were fed a total of 15 times from March 19 to April 17; during this period of approximately one month no eggs were laid by the three females. On April 17 the three nourished females were united with three well fed males; two of the three pairs were in copulation within less than five minutes. On April 20, or 72 hours after the males were mated with the females, two eggs were laid, and by the sixth postinsemination day there were 59 eggs present. This colony of three males and three females was fed on five successive days of each week from April 17 until May 28, at which time the colony was not fed again to determine the effect of starvation on the oviposition rate.

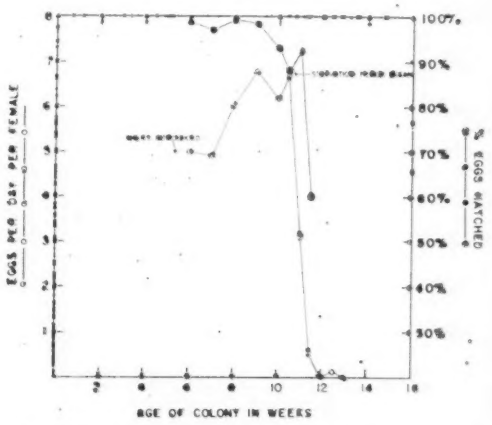


FIG. 6.—The productivity of a colony of *Hesperocimex sonorensis* consisting of three fed females and subsequently three males. These virgin females were fed five times per week for five weeks during which time no eggs were laid. After five weeks three well nourished males were introduced into the colony of three virgin females; eggs were produced within 72 hours. Feeding was continued for six additional weeks at which time starvation studies were instituted.

The data concerned with the rapid rise in oviposition rate and the decline in oviposition rate under conditions of starvation are to be found in figure 6. A study of this graph reveals a long period of reproductive inactivity of the well nourished virgin females and a rapid increase in the rate of oviposition from the third postinsemination day. By the sixth day of starvation this colony had essentially stopped egg production.

The data show that *Hesperocimex sonorensis* is similar to *Haematosiphon inodorus* (Lee, 1954) and to *Cimex lectularius* (Johnson, 1941) in that fed virgin females of the latter two species and *Hesperocimex sonorensis* are not capable of laying eggs.

The abdomens of well nourished virgin females become quite enlarged with large fat bodies showing through the semi-transparent abdominal sclerites and membranes. As might be expected, egg production was quite high from these females which had accumulated large nutritional reserves. This colony had the highest egg-laying rate of several colonies studied; the mean number of eggs laid per day per female was 5.79 during the first five weeks subsequent to mating. Nymphs hatched from 97.36% of the eggs laid during this period of time. Three days before the starvation studies were instituted the females laid 6.88 eggs per female per day; during the following three days post-starvation the laying dropped to 3.11 eggs per female per day and during the following three days: i.e. the fourth to sixth days of starvation inclusive, egg production dropped

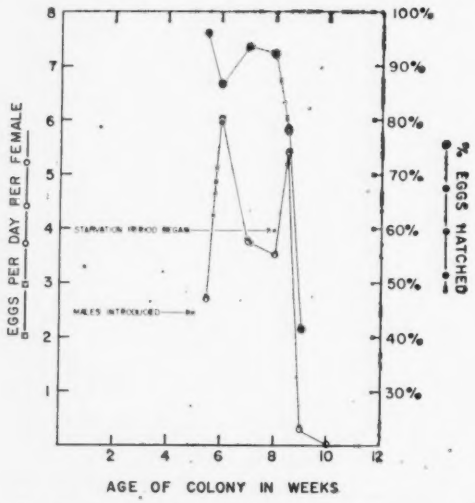


FIG. 7.—The productivity of a colony of *Hesperocimex sonorensis* consisting of 10 fed females and 20 fed males. The ten well nourished virgin females were reared for five weeks without males; twenty well fed, virgin males were introduced into this colony at the end of the fifth week; egg production began within 72 hours after the males were introduced. Feeding was continued for eight additional weeks at which time the colony was not fed again to determine the effects of starvation on egg production.

to 0.57 eggs per day per female with no eggs being laid during the subsequent five days and only one egg thereafter. These data would indicate that sustained reproduction is possible only if a constant blood supply is ingested and that virgin females do not lay eggs.

The above experiment was repeated using a larger number of individuals, and similar results were obtained with respect to the inability of fed virgins to lay eggs and the rapid increase in egg production subsequent to mating. Ten individually reared virgin females, which had emerged from April 13–25, were given their first blood meal on April 26 and were subsequently given the opportunity to feed to repletion on five successive days of each week until May 31. From April 26 to May 31 this colony of virgin females was permitted to feed to repletion on 26 days; during this 35-day period no eggs were laid. On June 1, 20 individually reared males which had emerged from April 11–18 were united with the fed virgin females; the males had been combined into one vial on May 28 and were fed on the four successive days of May 28–31 inclusive. No eggs were present on the second post-insemination day, but eight eggs were present on the third day after copulation with males. On the fourth day after copulation 45 eggs were laid. This colony was similar to the first colony of three females mentioned above in this study in that by the third day after copulation egg laying began and the production rate increased rapidly for the next two days. No eggs were laid by any of the fed virgins in either colony. This colony of ten females and 20 males was not fed after June 22 in order to determine how fast the egg production would diminish after feeding stopped. Starvation studies were imposed to simulate field conditions after the Purple Martin fledglings have left the nest to determine how long egg production would continue.

These data are summarized in figure 7. During the first 19 days of reproduction subsequent to exposure to males the ten females laid 724 eggs at the rate of 3.81 eggs per day per female. Nymphs hatched from 92.6% of these eggs. Egg production during the week prior to starvation was 3.52 eggs per female per day; during the first three days of starvation production was 5.40, and during the fourth to seventh days of starvation egg production dropped to 0.30 eggs per day per female. Only one egg was laid subsequent to the first week of starvation.

ACKNOWLEDGMENTS

The preceding studies were suggested by Dr. Robert L. Usinger in connection with the monograph of the cimicids of the world which is nearing completion in collaboration with Dr. G. F. Ferris. The writer also wishes to express with appreciation the suggestions and criticisms made by Drs. Deane P. Furman and Alden H. Miller of the University of California at Berkeley. (Research conducted at the University of California).

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thanks for a functional mobile laboratory which proved to be especially valuable under field conditions in Mexico. Without the financial and administrative support of the above it would not have been possible to have collected the type material or to have embarked on the studies described in this paper.

SUMMARY

The name *Hesperocimex sonorensis* has been proposed for the population of cimicids parasitizing the Purple Martin, *Progne subis hesperia*, of Sonora, Mexico. This species is distinguished from *Hesperocimex coloradensis* List, 1925, in general body size, color, and morphology of the male genitalia.

Several starvation studies were conducted to determine for what period of time *Hesperocimex sonorensis* could live without food. First instar nymphs permitted to feed to repletion molted and survived up to 63 days after the last blood meal. A colony of adult males and females which was not permitted to feed after molting to the adult survived up to 169 days for the males and 218 days for the females. A normally reproducing colony of males and females at approximately 75 days of age was starved in a manner intended to simulate the departure of the avian hosts from the nesting site; the adult males did not live more than 59 days, and the adult females were all dead by the 66th day of starvation.

The sex ratio of 301 nymphs emerging to the adult was found to be 1 female to 1.64 males, or 37.87% females and 62.12% males.

Fecundity studies indicate that well nourished virgin females are not capable of laying eggs in any form. Well nourished virgin females which were subsequently mated with males laid eggs at the rate of 5.79 per day per female for five consecutive weeks after exposure to males. The highest egg-laying rate was 6.88 eggs per day per female for a three-day period. The females in a colony of nine males and 14 females laid a total of 5,195 eggs over a period of 28 consecutive weeks; this is a mean of 371 eggs per female during their period of reproductive activity. Nymphs hatched from 92.47% of the eggs laid; therefore, the mean number of first instar nymphs produced was slightly over 343 per female.

Limited autogenous reproduction was found to be possible in this species. A colony of 15 unfed males and 15 unfed females produced nine eggs, eight of which hatched; this is a mean of 0.6 egg per female. Two colonies consisting of 13 unfed females and 23 fed males produced 25 eggs, all of which hatched; this is a mean of 1.92 eggs per female.

A study was conducted to determine if unfed males were capable of inseminating females with a relatively large quantity of viable sperms. Twenty-eight individually reared and unfed males were united with 14 females which had previously fed to repletion three times; after a period of one week together, the males were removed and the females fed five times per week. This colony of 14 fed females laid a total of 3,396 eggs during a period of 13 weeks subsequent to exposure to the 28 males. Maximum reproduction was attained for a period of 28 consecutive days during the third to sixth weeks inclusive, during which time 133 eggs were laid per female, or 4.75 eggs per female per day, for 28 consecutive days. Nymphs hatched from 91.93% of the eggs laid. After eight weeks there was a sharp decline in egg production, and by the 13th week essentially all egg laying had stopped. Males added to the colony at this time resulted in an immediate response in egg production to over 0.9 egg per day per female.

Egg production declined very rapidly if conditions of starvation were imposed upon a well fed colony producing eggs at a relatively rapid rate. In one colony studied egg production during the week prior to starvation was 3.52 eggs per female per day; during the fourth to seventh days of starvation egg production dropped to 0.30 eggs per day per female. Only one egg was laid subsequent to the first week of starvation.

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SOME EFFECTS OF GAMMA RADIATION ON TROGODERMA STERNALE JAYNE[1]

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The present study is an extension of work begun in 1955 on the comparative effects of radiation on various species of Coleoptera (see Howden, 1957). The first species investigated, *Onthophagus texanus* Schaeffer, belonged to that large group of Coleoptera that possess relatively fixed food habits and a low reproductive capacity. *Trogoderma sternale* (family Dermestidae), the species considered in this paper, is labile in its food needs and has a high reproductive capacity, which characterizes it as belonging to the group of insects that often are of economic importance.

Biology.—Beal (1956) has recently reviewed the economic species of *Trogoderma*. According to Beal (1954, 1956), *Trogoderma sternale* exists as a number of subspecies, which have a wide distribution over the southern and western United States. It is reported as occurring in a wide variety of niches. The specimens used in this study happen to be closely related to the subspecific form *T. sternale complex* Casey, and were collected in Knoxville, Tennessee, in some stored crushed corn.

In this species the sexes are easily distinguished both in the pupal and the adult stages, the females being half again as large as the males. Under the experimental conditions, the females in any one culture developed more rapidly than the males and emerged from one to two weeks earlier. Davis (1945, p. 354) states that "the imagoes of *T. versicolor* seem to emerge in cycles and the females outnumber the males until late in the period of emergence." Mating occurred shortly after the appearance of the males. The adults were short-lived, surviving from two to three weeks under laboratory conditions without flower pollen or other special food.

As has been reported for other dermestids (Davis, 1945) the number of eggs laid per female is variable, apparently depending on such factors as food, substrate, and population density, among others. In the present study, single isolated pairs produced up to 62 eggs per female whereas in controls which contained several females at one time, the average number of eggs was 27.

The whitish spherical eggs were laid singly in the pulverized food, hatching in approximately one week. The larvae were quite active, growing rapidly through six instars. After the sixth instar it was difficult to ascertain the remaining number of moults before pupation. The total number of moults varied, ranging from seven to fifteen. A similar variation has been noted in *Trogoderma versicolor* Cr. (Davis 1945, p. 354). This variation made it practically impossible to pick out larvae of exactly the same age or instar. New adults first appeared in the fifth and sixth months (mostly females during the fifth and males during the sixth). A few larvae remained unmetamorphosed for much longer periods, namely, 9 to 12 months.

METHODS

The *Trogoderma* larvae used in this experiment were sifted from a large mass culture maintained on corn, dried insects and purina chow. The larvae selected were at least fifth instar. They were placed in 4-oz. jars containing 20 grams of pulverized Purina chow, 1.5 grams of dried and pulverized insects, and five or six one-inch square pieces of dry paper toweling. Fifty larvae were placed in each culture jar. Thirty-two jars totaling 1600 larvae including controls were prepared. Two days later these were divided into two series, each of which was exposed to doses of gamma radiation from a cobalt-60 source. This facility was the same used in the previous study (Howden, 1957). Two replicates were used for each dose. Each series was exposed to 1000, 2000, 3000, 4000, 5000, 6000, and 10,000 roentgens delivered at the rate of 19 r/sec, this rate having diminished by radioactive decay from the 26 r/sec given the *Onthophagus* in 1955. One series received their doses in single exposures. The second series received one-fifth of their dose per day for five consecutive days. At the time of irradiation the 50 larvae together with their food substrate were transferred to a polyethylene cylinder which fitted into the cobalt facility. Under these conditions the 50 larvae in each replicate were exposed simultaneously. After exposure they were transferred back to the 4-oz. jars and kept in an incubator at a temperature of 29 ± 1° C.

At weekly intervals thereafter, jars were checked for emergence of adults. Upon emergence, the adults were removed, sexed, and transferred to fresh jars containing the same mixture of food material. The jars containing the newly emerged adults also were checked at weekly intervals for the appearance of F_1 larvae.

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TABLE 1

EFFECTS OF DOSE AND EXPOSURE ON TIME OF TRANSFORMATION OF LARVAE AND ON FERTILITY AS EXPRESSED BY NUMBER OF INDIVIDUALS.[a]

Dose		Instantaneous Exposure				Fractionated 5-day Exposure			
		Original larvae after 2 mos.	Original larvae after 6 mos.	No. of F_1 larvae in 2 mos.	No. of F_1, F_2 larvae in 6 mos.	Original larvae after 2 mos.	Original larvae after 6 mos.	No. of F_1 larvae in 2 mos.	No. of F_1, F_2 larvae in 6 mos.
Control	a)	38	0	331	820	11	0	569	700
	b)	45	0	64	553	22	0	555	824
1,000r	a)	37	16	176	486	24	15	178	485
	b)	40	18	20	225	20	0	196	588
2,000r	a)	38	28	136	358	26	14	22	79
	b)	45	17	20	122	25	13	5	54
3,000r	a)	35	27	178	286	21	17	86	434
	b)	40	15	63	288	34	12	20	28
4,000r	a)	40	26	4	49	23	18	4	48
	b)	42	22	0	0	29	21	4	7
5,000r	a)	46	31	0	0	27	19	32	192
	b)	43	30	0	0	24	14	0	0
6,000r	a)	38	14[b]	0	0	21	14	0	0
	b)	39	14[b]	0	0	25	18	0	0
10,000r	a)	5[b]	0[b]	0	0	12	3[b]	0	0
	b)	8[b]	0[b]	0	0	30	2[b]	0	0

[a]All replicates were started with 50 larvae.
[b]Mortality causing reduction in numbers before pupation.

These weekly checks were made over a two-month period, after which checking was less frequent. Final counts of the F_1 and F_2 generations were made six months after irradiation.

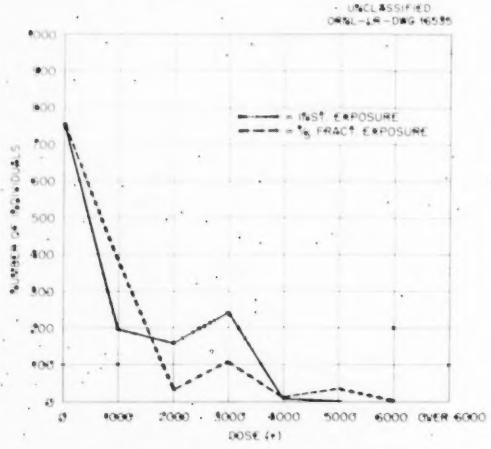

FIG. 1.—Total population (F_1) two months after irradiation.

RESULTS

In this study at least two effects were discernible. One was the differential growth of the population over the six-month period, and the second was the amount of delay in larval development caused by irradiation (Table 1). Due to variation in time of adult emergence or other factors causing variation in population size some effects, which might otherwise be attributable to differences resulting from single and fractionated exposures, were not always measurable.

Differences in population size at the various

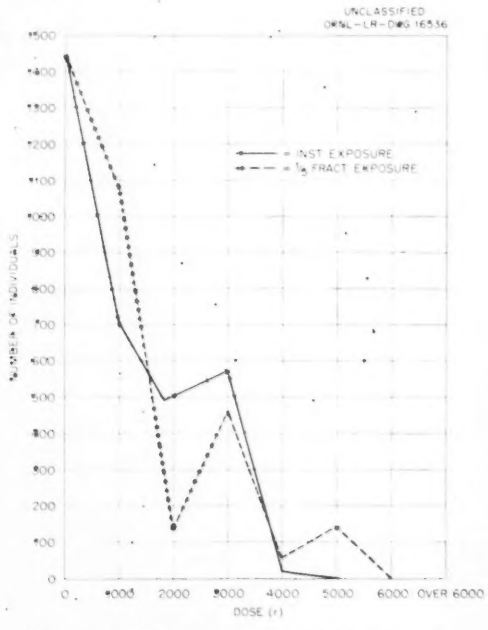

FIG. 2.—Total population (F_1 and F_2) six months after irradiation.

dose levels and differences in larval development time are presented in graphic form in Figures 1, 2, and 3, and summarized in Table 1. Figure 1 shows the effect of dose for both types of exposure on the size of the F_1 populations two months after irradiation. Figure 2 represents the same populations six months after irradiation while Figure 3 depicts the number of original larvae still present in each of the populations six months after irradiation.

DISCUSSION

From our data it is impossible to ascertain if there is any significant difference in the population sizes of the total versus the fractionated five-day irradiations in doses up to 5,000 r. There does seem to be a difference between single and fractionated doses needed for sterilization (Figures 1, 2). The *Trogoderma* were apparently sterilized by an instantaneous dose of 5,000 r since they were unable to reproduce, but when fractionated a dose of 6,000 r was needed to achieve the same

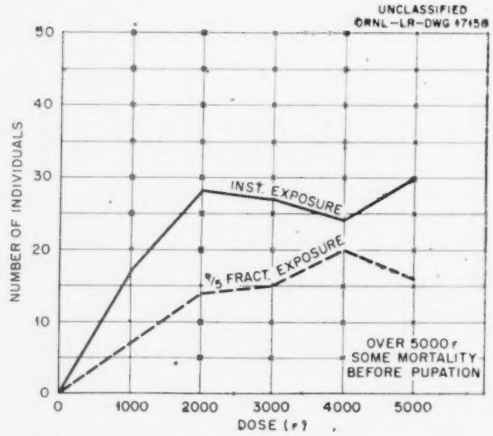

FIG. 3.—Number of untransformed larvae, 6 months post-irradiation.

results. Figure 3 also gives an indication that fractionation of the dose has less effect than instantaneous irradiation, since transformation was delayed to a greater degree in the latter case. At 10,000 r (Table 1) fractionation of the dose had a lesser effect on the larvae than did a single instantaneous dose. In two months' 86 percent of the larvae given a single exposure of 10,000 r had died, while only 28 percent of the larvae exposed over the five-day period died. At the end of six months there was 100 percent mortality in the one 10,000 r exposure and 94 percent mortality in the five-day series. (Perhaps this should be expected since Grosch (1954), using *Habrobracon* wasps, found that any prolongation of the delivery of the irradiation increased the amount needed for sterilization.) Fractionation of the dose, while supposedly causing as much cellular damage as the instantaneous dose, allows some recovery between irradiations, thus lessening the total effect. However, differences in fractionation versus instantaneous dose effects on population size below the sterilization level were not evident.

In considering the effects of the various doses whether given as an instantaneous or fractionated five-day exposure, it can be said that any dose had an adverse effect on the resulting population. In all cases, there was a reduction in population size, and at 3,000 and 4,000 r many of the adults resulting from the irradiated larvae were noticeably deformed. Crumpled elytra, malformed legs, and misshapen pronota were the most common deformities (for a more complete description of these types of deformities see Howden, 1957). Lessened activity also was apparent, particularly in the deformed individuals. As previously mentioned developmental time varies so that the females usually emerge a week or so before the males. In a situation such as this, if the female life span is shortened, perhaps by the effects of radiation, the female may die before the male has emerged, having the same effect as sterilization. This seemingly was one of the factors affecting the variations in population sizes noted in the present experiment and serves to illustrate that not just one factor, such as sterilization, should be considered, but that all of the ecological aspects need be investigated when considering the effects of radiation on species survival.

Reduction in population size at the lower levels of radiation, may not have been due to sterility as much as to lessened vitality, a suggestion originally proposed by Whiting and Bostian (1931). Less frequent matings and slightly shortened adult life span might be a factor in reducing the reproductive potential of any insect species. In *Trogoderma sternale* these effects may be magnified owing to the timing of the appearance of the adults. It was noted particularly in the 3,000 and 4,000 r treatments that the females often died before the males emerged, an event which eliminated reproduction as effectively as sterilization.

While the intent of the present study has been largely ecological, it seems fitting to mention a possible economic application of the present study in light of the recent paper by Hassett (1956). In this paper, Hassett considers the feasibility cost-wise of insect control by irradiation of stored products. His figures seem to imply the need for 16,000 roentgens for control. Not only the present work, but work by Bushland and Hopkins (1951, 1953), Grosch and Sullivan (1954), and others, indicate that much lower doses might be adequate.

SUMMARY

This paper discusses some of the aspects of the biology of *Trogoderma sternale* and the effects of

single and fractionated doses of gamma radiation on reproduction and larval development.

1. It was found that all doses delivered to full grown larvae affected reproduction adversely.

2. It is thought that reduction in population size at doses of 1,000 to 4,000 r may be explainable in terms of lowered vitality and/or morphological deformities affecting the mating behavior.

3. There was no apparent difference in effects on numbers of offspring between instantaneous and fractionated exposures below 5,000 r.

4. There was a difference in effect of fractionated and instantaneous exposures at 5,000 and 6,000 r. At instantaneous exposures of 5,000 r and above there was no reproduction, but, when fractionated, exposures of 6,000 r was needed to prevent reproduction.

5. Larval development was delayed more by instantaneous doses than fractionated ones.

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NOTE ON SURVIVAL AND FEEDING OF NEWLY HATCHED LARVAE OF CTENICERA AERIPENNIS DESTRUCTOR (BROWN) (COLEOPTERA: ELATERIDAE)[1]

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Strickland (1933, 1939) found a high mortality of larvae of *Ctenicera aeripennis destructor* (Brown) in the field during the first two summers of life. When the larvae were provided with grains or cultivated grasses as food during this period, an average of 35 percent and 62 percent, respectively, survived. Only 2 percent survived on plants of Russian pigweed and 10 percent on flax. This is a report on survival of larvae of this species during the first 12 weeks of life when they were fed on wheat, flax, barley, and rye seed and when they were kept without food in sterilized soil under controlled conditions.

To obtain eggs, several adults of both sexes were maintained at 68 ± 2° F. in a closed 8-ounce glass jar containing a piece of carrot and moist soil that had been passed through a 70-mesh screen. When oviposition had begun, the soil was washed through a 70-mesh screen with tap water every 2 or 3 days to collect the eggs.

The screen was examined under a binocular microscope and the eggs were removed with a small sable-hair paint brush. The eggs were incubated on small circles of moist blotting paper in closed petri dishes at 68° F. and 75 percent relative humidity. The eggs hatched 16 to 21 days after their removal from the soil.

Within 24 hours of hatching, the larvae were transferred to individual 1-ounce salve tins containing oven-dried clay loam soil brought to 27 percent moisture saturation with distilled water. Each tin contained one seed of wheat, barley, or rye, or five seeds of flax, or no food.

To determine whether larvae could survive only on dead organic matter present in the soil, one series was reared in sterilized soil without food. The soil was heated to 212° F. for 4 hours and allowed to cool to room temperature. This was repeated on 3 successive days. The soil was brought to 27 percent moisture saturation with sterile distilled water. The tins containing the larvae were closed and placed in a constant temperature cabinet at 68° F. and 75 percent relative humidity.

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TABLE I

NUMBERS OUT OF 100 LARVAE OF *C. a. destructor* SURVIVING UP TO 12 WEEKS FROM HATCHING WHEN PROVIDED WITH VARIOUS SEEDS OR WITH SOIL ONLY

FOOD	WEEKS AFTER HATCHING						AVERAGE PER REPLICATE[a]
	2	4	6	8	10	12	
Flax	55	31	28	22	19	17	1 87
Wheat	46	23	14	11	8	8	1 34
Rye	22	13	13	9	6	6	1 25
Barley	26	14	6	5	4	3	0 99
No food, unsterilized soil	9	0	0	0	0	0	0 71
sterilized soil	0	0	0	0	0	0	0 71
L.S.D. at 5% level							0 59

[a]Original values transformed, using the formula $\sqrt{X + 0.5}$.

Five replicates of 20 larvae each were used for each test. Every 2 weeks for a period of 12 weeks, mortality and feeding activity were recorded and fresh soil and food were provided.

A square-root transformation was applied to the survival data and an arcsine transformation to the feeding data, after which an analysis of variance was carried out. Differences in survival and in incidence of feeding were determined by means of the F test at the 5 percent level.

Significantly more larvae survived on flax than on rye or barley (Table I). Survival on wheat was not significantly different from that on flax, rye, or barley. On rye or barley, survival was not significantly higher than when no food was added to the soil. Mortality was greatest during the first 2 weeks and continued at a high level until the end of the sixth week. No larvae survived after the second week in unsterilized or in sterilized soil without added food, suggesting that they were incapable of surviving on living microorganisms or on dead organic matter in the soil, or on both.

Analysis of the data showed that the larvae fed as often on any one food as on the others. The periods of greatest feeding occurred at different times with different foods (Table II). This suggests that the feeding behaviour of the larvae is influenced by the food value of the seeds or by their attraction for the larvae, or both.

Contrary to results obtained by Strickland under field conditions (1933, 1939), this investigation indicated that under controlled conditions flax is as good as wheat and superior to rye or barley for the survival of young larvae of this species. It also showed that survival is less under these conditions than that found by Strickland in the field.

TABLE II

PERCENTAGES OF SURVIVING LARVAE (ANGULAR TRANSFORMATIONS) OF *C. a. destructor* FEEDING ON VARIOUS SEEDS DURING 2-WEEK PERIODS UP TO 12 WEEKS FROM HATCHING

FOOD	WEEKS AFTER HATCHING						AVERAGE
	2	4	6	8	10	12	
Flax	33 8	57 4	38 6	50 2	48 4	53 7	47 0
Rye	25 1	51 3	28 7	47 9	65 6	35 1	42 3
Wheat	29 3	48 4	36 9	47 3	30 0	30 0	37 0
Barley	28 7	0 0	45 0	26 6	30 0	54 9	30 9
L.S.D. at 5% level							16 5

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OBSERVATIONS ON REPRODUCTION AND DEVELOPMENT IN COCKROACHES[1]

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Although various information has been published previously on reproduction and development in the common species of cockroaches, similar data on less common cockroaches are comparatively meager. During the last few years we have accumulated considerable miscellaneous biological information on seventeen species of cockroaches. This material has been reduced to a number of mean values which are presented hereinafter with estimates of their variability. Although simultaneous comparisons of our data with those of other workers would be desirable, economy of space precludes our increasing the tabular material by including comparative values from the literature.

The following references may be consulted for pertinent biological data for some of the common domiciliary cockroaches: Cottam (1922), von Fischer (1928), Gier (1947), Gould and Deay (1938, 1940), Griffiths and Tauber (1942), Hafez and Afifi (1956), Klein (1933), Landowski (1937), Morisset (1946), Nigam (1933), Pope (1953), Qadri (1938), Rau (1924, 1940), Ricci (1950), Ross (1929), Seín (1923), Wille (1920), Woodruff (1938, 1938a), Zabiński (1929, 1936).

MATERIAL AND METHODS

Original observations have been made on the following species of cockroaches which are grouped below according to their oviposition behavior (see Roth and Willis, 1954, 1955).

Group I.—Oviparous species that drop their oöthecae shortly after formation: *Blatta orientalis* Linnaeus, *Cariblatta lutea minima* Hebard, *Eurycotis floridana* (Walker), *Neostylopyga rhombifolia* (Stoll), *Periplaneta americana* (Linnaeus), *Periplaneta australasiae* (Fabricius), *Periplaneta brunnea* Burmeister, *Periplaneta fuliginosa* (Serville), and *Supella supellectilium* (Serville).

Group II.—Oviparous species that carry their oöthecae externally until, or shortly before, hatching: *Blattella germanica* (Linnaeus) and *Blattella vaga* Hebard.

Group III.—Cockroaches which deposit their oöthecae internally in a brood sac where the eggs remain until hatching: False ovoviviparous species (see Roth and Willis, 1955), *Blaberus craniifer* Burmeister, *Byrsotria fumigata* (Guérin), *Leucophaea maderae* (Fabricius), *Nauphoeta cinerea* (Olivier), and *Pycnoscelus surinamensis* (Linnaeus); and the false viviparous species (see Roth and Willis, 1957), *Diploptera punctata* (Eschscholtz) (= *D. dytiscoides* (Serville) [Princis, 1950]).

The preoviposition period is based on the production of the first oötheca by females that were kept with males from the time of emergence; the time to production of the first oötheca is lengthened if the female does not mate (Roth and Willis, 1956). Egg development was timed from the day each oötheca was seen being formed. Oöthecae that were dropped by oviparous species were placed individually in shell vials until the eggs hatched. Females of the two species of *Blattella* and of the so-called "viviparous" cockroaches were isolated in beakers while they carried oöthecae.

Nymphal development was determined for individual insects, kept in 250–500 ml beakers, and for groups of insects which were kept in 1000 ml. beakers or larger glass jars. The bottoms of the containers were lined with filter paper and the tops were covered with cloth. Individuals of species that tended to eat the cast skins were marked with colored lacquer so that moults would not be overlooked. Lacquer applied to the dorsal surface of the legs of each nymphal stage remained visible throughout each instar.

Food (Purina Dog Chow Checkers) and water were provided continuously. *Pycnoscelus surinamensis* was also provided with fresh lettuce; however, we have since found it unnecessary to supplement the diet of *Pycnoscelus* with lettuce in order to maintain a colony.

The temperature and humidity conditions that prevailed during the different experiments were not all alike. The observed room conditions are noted under each species in the section on results.

RESULTS

The various species of cockroaches are arranged below alphabetically by type of oviposition behavior as indicated in the preceding section. The oviparous species that drop their oöthecae usually form another oötheca within a few days thereafter, and the interval between successive oöthecae is short, usually much shorter than the period of incubation. The other species, which carry their oöthecae about with them until the eggs hatch, are prevented by this behavior from forming another oötheca until the current one is dropped at hatching or is aborted. Among these latter species, the interval between successive oöthecae,

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when these are carried to full term, is somewhat longer than the period of incubation.

GROUP I

Blatta orientalis.—All observations were made in a laboratory where the temperature was maintained at about 30° C. except for occasional hot days in summer when it reached 36° C. The humidity was uncontrolled.

matured more rapidly than females except for the progeny of mated parthenotes that were offspring of virgin females.

Zabiński (1929, 1936) suggested that regeneration of injured appendages increased the number of moults in cockroaches. For this reason we analyzed the data separately for normal insects with five-segmented tarsi and for injured insects that had regenerated legs with only four seg-

TABLE I

COMPARATIVE REPRODUCTIVE DATA FROM OVIPARIOUS COCKROACHES THAT DROP THEIR OÖTHECAE SHORTLY AFTER FORMATION

TYPE OF OBSERVATION	MEAN VALUES ± STANDARD ERRORS													
	Blatta orientalis	N[a]	*Eurycotis floridana*	N[a]	*Periplaneta americana*	N[a]	*Periplaneta australasiae*	N[a]	*Periplaneta brunnea*	N[a]	*Periplaneta fuliginosa*	N[a]	*Supella supellectilium*	N[a]
Oöthecae per Female	.....		.....		.....		.....		.....		.....		10.8±0.5	35
Preoviposition Period, Days	12.2±1.1	8	55 ±3.9	19	.....		24 ±3.9	10	9.5±0.5	2	16.3±0.9	3	10.4±0.3	35
Intervals between successive Oöthecae, Days	.....		8.3±0.5[c]	61	.....		9.8±0.6	85	3.8±0.2	29[e]	10.6±2.3	13	6.4±0.2	343
													5.9±0.1	308[f]
													11.4±1.1	35[g]
Incubation Period, Days	43.7±0.2	32[c]	48.4±0.7	18	34.0±0.2	277[f]	40.3±0.1	89	39.5±0.3	6[e]	.....		39.9±0.05	303
	44.6±1.4	7[d]			37.6±0.5	50[g]								
Eggs per Oötheca	.....		20.9±0.5	16	.....		23.8±0.2	219	.....		19.7±0.9	15	15.5±0.1	372
Eggs Hatched per Oötheca	15.4±0.2	32	18.0±1.1	16	11.2±0.5	50[g]	16.1±0.7	85	23.9±0.5 9.6±2.1	22[h] 26[i]	.....		12.2±0.1	358
Developed, Unhatched Eggs per Oötheca	.....		0.7±0.3	15	.....		3.6±0.4	85	.....		.....		.....	
Undeveloped Eggs per Oötheca	.....		1.9±0.8	15	.....		4.3±0.5	85	.....		.....		.....	
Percentage of Hatched Insects that Matured	94% 91%	492[c] 80[d]	.....		84%	561[g]	55%	257	.....		51%	69	85%	210
Sex Ratio[b] ♀♀:♂♂	1:1.05 1:1.15	464[c] 73[d]	1:1.13	181	1.08:1	468[g]	1:1.09	138	.....		1:1.33	35	1.32:1	179

[a]Number of insects or oöthecae. [b]Based on only those insects that matured. [c]Produced by mated females of bi-parental stock. [d]Produced by mated parthenotes that were offspring of virgin females. [e]This experiment was stopped after 110 days before more than 5 oöthecae had been produced by any one female. [f]Produced parthenogenetically by virgin females. [g]Based on only those oöthecae that were produced and had hatched by the last day of summer. See text. [h]Hatch based on all oöthecae produced by first female except the last 17 oöthecae which were damaged so the eggs could not develop. [i]Hatch based on all oöthecae produced by the second female. Twelve of these oöthecae did not hatch. [j]Exclusive of the interval between the penultimate and last oötheca. [k]Interval between penultimate and last oötheca.

Males and females that had been isolated at emergence mated readily when first placed together from four to nine days later. The mean duration of copulation was 40±3.5 minutes (N=8)[3]. The observed reproductive performance of this species is given in table I.

All nymphal stages of this species were unable to climb vertical glass walls. Data on nymphal development are given in table II. Males

mented tarsi. The small numbers of insects with regenerated appendages do not enable us to substantiate or refute Zabiński's hypothesis. However, the more rapid development of nymphs reared in groups compared to those reared separately is in agreement with similar observations made by Landowski (1937).

Cariblatta lutea minima.—Limited data on reproduction and nymphal development are given in table III. These observations were made in an air conditioned, walk-in incubator at 27° C. and 70% relative humidity. The oöthecae were

[3]N = the number of insects; the figure at the right of the ± is the standard error.

kept on moist cotton until the eggs hatched. Females required about 5 more days than males to mature.

Eurycotis floridana.—All observations except those on virgin females were made in a laboratory where the temperature was 30° C. except for occasional short periods when it reached 36° C. The humidity was uncontrolled. Virgin females were maintained in an air-conditioned insectary at 24° C. and 50–60% relative humidity.

Adults of each sex were isolated upon emergence and later placed together in a 1000 ml beaker for several hours each day until copulation occurred. One pair mated on the eighteenth day and two pairs mated on the nineteenth day after emergence. The mating behavior of this species has been described by Roth and Willis (1954). Since that publication we have seen many males courting females in mid-afternoon. Initiation of copula was not observed, but one pair remained in copulo for over an hour and another pair for over two hours. Spermatophore remains were dropped by these females four days later. Among the mated pairs set up to provide information on reproduction, as many as four spermatophores were found in 110 days; this indicates at least four successive matings by the same pair of insects. The spermatophores were found at intervals of from four to forty-one days. Reproductive data from females kept with males are given in table I.

Virgin females were isolated upon emergence and their eggs were examined for evidence of parthenogenetic development. Females that were observed from emergence until death lived 229±44 days (N = 10) and produced 5.8±1.7 oöthecae per female of which 3.4±1.2, or 59%, contained eggs that developed parthenogenetically. Eight other females that were still alive when the experiment was terminated were observed for an average of 377±20 days. During this period they produced an average of 13.9±2.6 oöthecae per female of which 7.1±1.9, or 51%, contained eggs that developed parthenogenetically. Parthenotes hatched from only three oöthecae and most died within a short time. However, at the time this was written two large nymphs were still alive; both were females. Failure of most of the eggs to hatch cannot be attributed to there being too few mature embryos to split the keel of the oötheca (cf. *Blattella germanica*, Roth and Willis, 1956) because in many instances practically every egg developed in oöthecae in which any development occurred.

The nymphs of *Eurycotis floridana* can climb vertical glass walls at birth. Data on nymphal

TABLE II

NYMPHAL DEVELOPMENT IN *Blatta orientalis*

	DURATION IN DAYS[a] OF EACH INSTAR AND NYMPHAL STAGE OF INSECTS REARED ALONE							
	FEMALES				MALES			
INSTAR	Normal	N[b]	Regenerated	N[b]	Normal	N[b]	Regenerated	N[b]
1	9.1± 0.3	7	9.5± 0.5	4	9.1± 0.4	12	8.5± 0.2	4
2	11.1± 0.8	7	12.8± 0.6	4	10.5± 0.4	12	11.5± 1.2	4
3	11.3± 0.3	7	12.2± 0.8	4	11.7± 0.3	12	14.8± 2.4	4
4	15.4± 0.7	7	15.2± 0.6	4	15.3± 0.7	12	17.0± 3.5	4
5	22.9± 1.4	7	19.5± 1.2	4	17.2± 0.8	12	20.5± 3.2	4
6	32 ± 4.5	7	29.2± 2.8	4	27.9± 1.9	12	32 ± 5.9	4
7	40 ± 4.1	7	37.8± 3.2	4	51 ± 8.6	12	64 ±20	4
8	79 ±13	7	52 ±14	4	38.4± 3.8	10	56 ± 9.9	4
9	42 ± 7.5	7	23.2± 2.5	4	.....		46 ±11	3
10	28.5± 2.5	2	.....		.....		82	1
NYMPHAL STAGE								
7 Moults	.....		.....		164±13	2		
8 Moults	.....		.....		177±15	10	264	1
9 Moults	267 ±12	5	212 ±18	4	.....		233 ± 9	2
10 Moults	282 ±30	2	.....		.....		382	1

DURATION IN DAYS[a] OF NYMPHAL DEVELOPMENT OF INSECTS REARED IN GROUPS

Females	N[b]	Males	N[b]
165±3.4	226	146±2.8	238
126±4.8	34[c]	128±3.8	39[c]

[a]Mean ± standard error.
[b]Number of insects.
[c]Progeny of mated parthenotes that were offspring of virgin females.

development are given in table IV. Both sexes mature at about the same rate. The few insects with regenerated legs matured in less time than normal insects. Nymphs reared in groups matured more rapidly than isolated individuals.

Neostylopyga rhombifolia.—Limited data on reproduction and nymphal development are given in table III. Females took longer to mature than did males. These observations were made at 27° C. and 70% relative humidity.

Twelve females were isolated as virgins at emergence for determination of parthenogenesis. They were maintained at 24° C. and 50–60% relative humidity. Two of these lived only two weeks and produced no oöthecae. The remaining ten females lived 156±42 days. Three of these produced no eggs; six females produced 13 oöthecae in which no eggs developed; only one female produced eggs that developed (in two oöthecae). Eight nymphs hatched from one oötheca but none survived.

Periplaneta americana.—All observations were made at about 30° C. except for occasional hot days when the temperature reached 36° C. The humidity was uncontrolled.

Males and females that had been isolated at

TABLE III

DATA ON REPRODUCTION AND NYMPHAL DEVELOPMENT IN THREE SPECIES OF COCKROACHES

TYPE OF OBSERVATION	MEAN VALUES ± STANDARD ERRORS					
	Byrsotria fumigata[a]	N[b]	*Cariblatta lutea minima*[c]	N[b]	*Neostylopyga rhombifolia*[c]	N[b]
Incubation Period, Days			26.0±0.5	8		
Eggs Hatched per Oötheca	25.4±2.8	8	11.8±0.1	16	21.8±2.6	21
Period of Development of Nymphs Reared in Groups, Days						
Females	275 ±3.7	9	65.1±1.2	24	302 ±1.7	39
Males	239 ±3.0	10	59.8±1.8	11	286 ±2.6	22

[a]A false ovoviviparous species belonging to the Blaberinae.
[b]Number of oöthecae and insects.
[c]Oviparous species that drop their oöthecae.

TABLE IV

NYMPHAL DEVELOPMENT IN *Eurycotis floridana*

INSTAR	DURATION IN DAYS[a] OF EACH INSTAR AND NYMPHAL STAGE OF INSECTS REARED ALONE							
	FEMALES				MALES			
	Normal	N[b]	Regenerated[c]	N[b]	Normal	N[b]	Regenerated[c]	N[b]
1	11.8±0.2	27	13.0±1.4	5	12.1±0.1	31	11.8±0.2	5
2	10.6±0.1	27	11.2±0.5	5	10.7±0.1	31	10.2±0.2	5
3	11.2±0.2	27	12.0±0.3	5	11.3±0.2	31	12.4±0.2	5
4	12.7±0.2	27	12.2±0.6	5	13.0±0.3	31	11.6±0.4	5
5	16.9±0.7	27	14.8±1.4	5	17.6±0.8	31	15.4±1.0	5
6	19.4±1.0	27	20.0±1.3	5	19.1±0.9	31	16.2±0.4	5
7	29.8±1.4	26	25.6±1.2	5	28.0±1.4	27	23.4±0.8	5
8	36	1						
NYMPHAL STAGE								
6 Moults	99	1			96.2±1.5	4		
7 Moults	112.7±2.6	25	108.8±2.4	5	109.8±2.4	27	101.0±1.5	5
8 Moults	134	1						

DURATION IN DAYS[a] OF NYMPHAL DEVELOPMENT OF INSECTS REARED IN GROUPS

Females	N[b]	Males	N[b]
102.2±0.9	85	98.8±0.6	96

[a]Mean ± standard error.
[b]Number of insects.

emergence copulated seven days later when placed together. Pairs remained in copulo about an hour. Limited data on reproduction in this species are given in table I.

Data on nymphal development in *Periplaneta americana* are given in table V. Nymphs are unable to climb vertical glass walls until after the sixth or seventh moult. Nymphs with regenerated legs did not require a longer period to mature than normal insects; however, nymphs reared in groups matured in less time than those reared separately.

Data on reproduction by mated females of this species are given in table I. Twenty-six virgin females were isolated at emergence for determination of parthenogenesis. Twelve of these died within two to three weeks without having produced oöthecae. Three females produced oöthecae that were damaged so that egg development could not be checked. Of the remaining eleven females, four produced within their lifespan of 33±4 days only one oötheca each; no eggs developed in these oöthecae. The other seven females produced in 173±56 days,

TABLE V

NYMPHAL DEVELOPMENT IN *Periplaneta americana*

INSTAR	DURATION IN DAYS[a] OF EACH INSTAR AND NYMPHAL STAGE OF INSECTS REARED ALONE							
	FEMALES				MALES			
	Normal	N[b]	Regenerated	N[b]	Normal	N[b]	Regenerated	N[b]
1	7.5±0.1	13	7.8±0.3	11	7.4±0.2	16	7.0±0.0	3
2	9.7±0.4	13	10.4±0.3	11	10.5±0.5	16	10.3±0.3	3
3	13.7±1.8	13	13.4±1.3	11	12.9±0.7	16	13.7±3.3	3
4	19.5±2.2	13	19.5±2.2	11	19.6±2.1	16	18 ±5.0	3
5	27.6±2.3	13	27.5±3.8	11	24.9±2.5	16	24 ±4.8	3
6	25.2±2.3	13	28.7±2.7	11	33 ±4.2	16	21.3±1.7	3
7	28.9±3.8	13	37 ±5.2	11	33 ±4.5	16	30 ±4.4	3
8	40 ±5.2	13	39.2±3.9	11	40.6±3.1	16	45 ±7.6	3
9	42 ±7.1	13	37 ±4.8	11	37.7±3.3	16	31 ±6.4	3
10	48 ±8.7	12	33 ±6.4	11	39.4±3.5	16	20 ±7.6	3
11	44 ±8.4	10	42 ±5.2	10	43 ±4.8	13	11 ±16	3
12	42 ±9.4	5	41 ±6.4	8	49 ±4.4	9	36 ±12	2
13	25.3±1.8	3	81	1	36.8±2.2	4	11	1
NYMPHAL STAGE								
9 Moults	143	1						
10 Moults	180 ±26	2	218	1	212 ±5.8	3		
11 Moults	283 ±31	5	261 ±16	2	294 ±19	4	280	1
12 Moults	410 ±12	2	339 ±22	7	375 ±36	5	243	1
13 Moults	391 ±29	3	507	1	400 ±11	4	337	1

DURATION IN DAYS[a] OF NYMPHAL DEVELOPMENT OF INSECTS REARED IN GROUPS

Females	N[b]	Males	N[b]
197.2±0.8	825[c]	170.6±2.0	225[d]
160.5±2.1	243[d]		

[a]Mean ± standard error.
[b]Number of insects.
[c]Progeny of virgin females.
[d]Progeny of mated parthenotes that were offspring of virgin females.

Periplaneta australasiae.—All observations except those on virgin females were made at about 30° C. with occasional highs of 36° C.; the humidity was uncontrolled. Virgin females were maintained at 24° C. and 50-60% relative humidity.

Males were seen attempting to mate at five days of age. They raised their wings and flexed their abdomens ventrally in behavior similar to that of males of *P. americana* (see Roth and Willis, 1952, 1954).

the average period they were observed, a total of 80 oöthecae; fourteen of these contained some eggs that developed. None of the developed embryos hatched.

Data on nymphal development are given in table VI. Groups of nymphs reared together matured more rapidly than those kept alone. The first instar nymphs can climb glass.

Periplaneta brunnea.—Observations of fertile females were started at about 30° C., but by the end of summer these insects were removed to a

private home where the temperature varied between 19° and 24° C. The humidity was uncontrolled. Virgin females were maintained at 24° C. and 50–60% relative humidity.

Only two fertile females were available at the time these observations were made. Data on reproduction of these females are given in table I. When these insects were removed to a lower average temperature during the experiment, the following changes from the data in table I were noted. The average intervals between the last six oöthecae produced by each female was 13.0±

TABLE VI

NYMPHAL DEVELOPMENT IN *Periplaneta australasiae* ALL INSECTS HAD REGENERATED LEGS

INSTAR	DURATION IN DAYS[a] OF EACH INSTAR AND NYMPHAL STAGE OF INSECTS REARED ALONE			
	Females	N[b]	Males	N[b]
1	11.2±1.4	10	12.8±2.7	5
2	16.4±2.3	10	18 ±5.6	5
3	19.9±1.5	10	20 ±4.0	5
4	22.8±3.6	10	33 ±6.4	5
5	32 ±5.6	10	37 ±11	5
6	32.0±3.2	10	44 ±15	5
7	35 ±6.1	10	31.8±2.2	5
8	32.7±2.5	10	28.6±2.1	5
9	37.0±2.9	10	38 ±5.2	5
10	37.9±3.2	10	48 ±11	5
11	41 ±4.4	10	25	1
12	64 ±6.8	2	.....	
Nymphal Stage				
10 Moults	.....		306±39	4
11 Moults	253±10	3	365	1
12 Moults	410±25	2	.....	

DURATION IN DAYS[a] OF NYMPHAL DEVELOPMENT OF INSECTS REARED IN GROUPS

Females	N[b]	Males	N[b]
213±7.5	66	198±6.6	72

[a]Mean ± standard error. [b]Number of insects.

1.6 days (N = 10). The average incubation period of the last five oöthecae from each female from which eggs hatched was 80.5±1.9 days (N = 10).

Data on parthenogenesis in this species were obtained from 29 virgin females. Twenty-one of these lived an average of 98±24 days during which time they produced 4.4±1.4 oöthecae per female; of these 0.86±0.42 oöthecae per female contained eggs that developed. Nineteen nymphs hatched from one oötheca. The eight other females, which were still alive when the observations were terminated, were observed for 309±9 days. During this period they produced 10.6 ± 3.4 oöthecae per female; 5.1±1.6 oöthecae per female contained eggs that developed. Of the 29 females, 15 produced eggs that developed parthenogenetically in 38% of the 173 oöthecae examined. Eggs hatched from 8.7% of the oöthecae examined. Of the 208 nymphs that hatched, 66 have matured; all were females; 82 additional nymphs were still alive at time of writing.

The longevity of several adults of *P. brunnea* is given in table X.

Periplaneta fuliginosa.—All observations were made at about 30° C. except for a few days in summer when the temperature reached 36° C. The humidity was uncontrolled.

Males of this species attempted to mate five days after emergence. Reproductive data are given in table I. Data on nymphal development are given in table VII. Nymphs reared in groups matured much more rapidly than isolated individuals. Nymphs can climb glass at birth.

Supella supellectilium.—All observations were made during the fall, winter, and spring months when the temperature was maintained at about 30° C. The humidity was uncontrolled.

One female was seen in copulo three days after emergence as an adult. The youngest male seen in copula was five days old. Pairs were seen mating only three times. Copulation lasted at least 20 minutes; initiation of the act was not observed. Courting and initiation of copulation has been described by Roth (1952). If the male is successful in making connection with the female, they swing about into the opposed position facing opposite directions. While in copulo the male held his wings raised at an angle of about 30°. Males were seen feeding on the secretion of the dorsal gland of other males that had raised their wings while courting females.

About 18 hours elapsed between the beginning of the formation of the oötheca and its deposition. Other data on reproduction are given in table I. The variation in the numbers of eggs in successive oöthecae is shown in figure 1. The maximum hatch was reached with the seventh oötheca (fig. 1).

The longevity of adults of this species is given in table X, as is the relation between the longevity of females and their fecundity. This relationship is not as clear cut in this species as in some of the others. However, there is some slight suggestion that females that lived longer tended to produce more oöthecae. The period between formation of the last oötheca and death of the female did not change appreciably as the females grew older.

Data on nymphal development are given in table VIII. Both sexes matured in about the same length of time. The nymphs can climb glass upon hatching.

GROUP II

Blattella germanica.—All observations were made during the cool months of the year when

the insectary temperature was maintained at about 30° C. The humidity was uncontrolled.

Most of the females of this species rotated their oötheeae so that the keel was toward the female's right. A few females were seen that had rotated the oötheca with the keel toward their left or had retained the oötheca with the keel dorsal or only slightly tilted toward the side. Data on reproduction are given in table IX. Data on adult longevity are given in table X.

were examined as they matured for the presence of regenerated legs. Six adults had one regenerated tarsus; these insects had moulted only six times (cf. Woodruff and Seamans, 1939). Information on nymphal development is given in table XI. Both sexes matured in about the same length of time.

Blattella vaga.—Observations were made at about 30° C. except for occasional highs of 36° C. The humidity was uncontrolled.

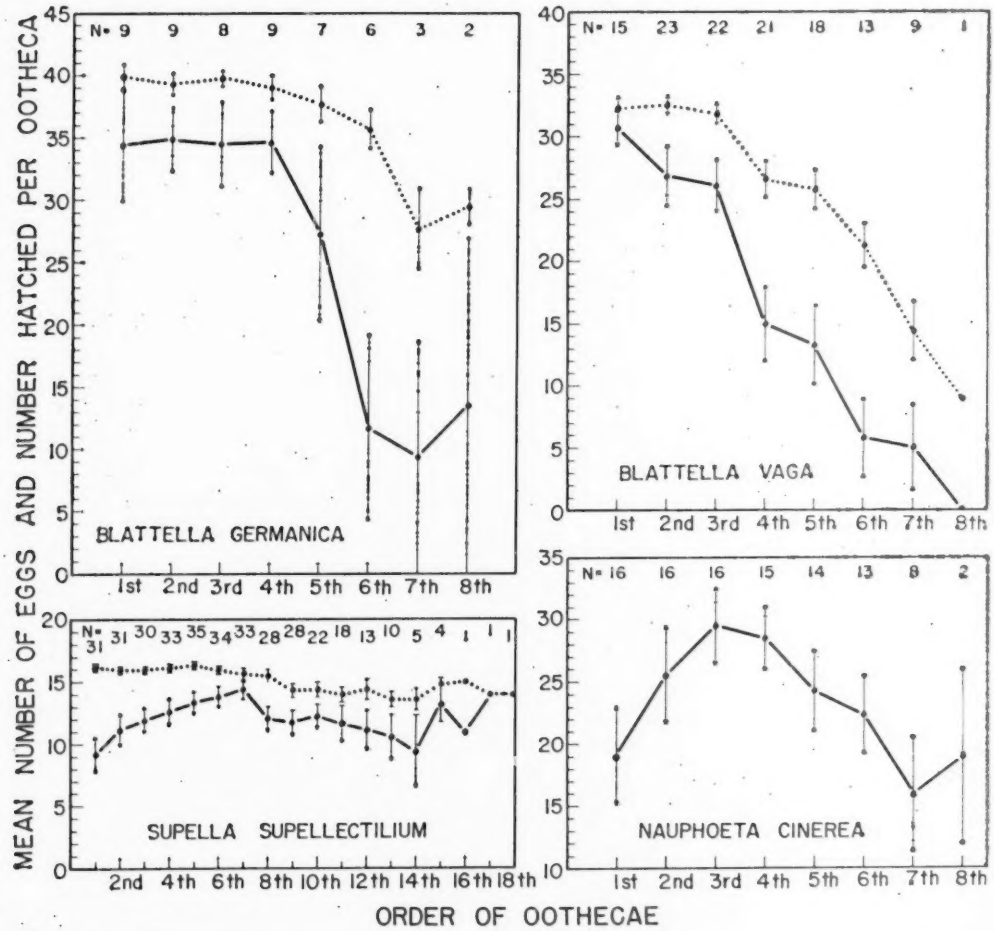
MEAN NUMBER OF EGGS AND NUMBER HATCHED PER OOTHECA
ORDER OF OOTHECAE
BLATTELLA GERMANICA
N= 9 9 8 9 7 6 3 2
1st 2nd 3rd 4th 5th 6th 7th 8th
BLATTELLA VAGA
N= 15 23 22 21 18 13 9 1
1st 2nd 3rd 4th 5th 6th 7th 8th
SUPELLA SUPELLECTILIUM
N= 31 31 30 33 35 34 33 28 28 22 18 13 10 5 4 1 1 1
2nd 4th 6th 8th 10th 12th 14th 16th 18th
NAUPHOETA CINEREA
N= 16 16 16 15 14 13 8 2
1st 2nd 3rd 4th 5th 6th 7th 8th

FIG. 1.—The number of eggs produced and the number that hatched per oötheca in relation to the sequence of oöthecal formation. Dotted lines are numbers of eggs per oötheca; solid lines are numbers of eggs that hatched per oötheca. N = the number of oötheeae observed. The vertical capped lines indicate one standard error.

The longer-lived females tended to produce more oötheeae. The number of eggs per oötheca dropped with succeeding oötheeae after the fourth (fig. 1).

Nymphs were able to climb vertical glass walls at birth. All of the 109 nymphs reared separately

One female that was isolated upon emergence copulated when placed with a male three days later. Males also copulated when three days old. Other females mated four to nine days after becoming adult. The mean duration of copulation was 80 ± 4.9 minutes (N = 7). Mated females

dropped the spermatophore within 24 hours after copulation. Several spermatophores were seen in the beakers containing mated pairs during the course of the experiment. Males that had been previously mated were introduced to new females after 24 hours at which time they mated readily. Shorter intervals between matings were not tried. Females were seen in copulo a few hours after dropping an oötheca.

Comparative data on reproduction of mated and unmated females are given in table IX. Only one virgin female produced eggs that developed parthenogenetically; these did not hatch. Half of the oötheca produced by unmated females were carried for one day or less.

There was considerable variation in the length of the periods between formation of the last oötheca and death of the female, and no recognizable trend is apparent.

As in *Blattella germanica*, nymphs of *B. vaga* moulted five to seven times after shedding the embryonic membrane. The nymphs can climb vertical glass walls immediately after birth. Data on nymphal development are given in table XII. In this species the female matured more rapidly than the male. The development time for individuals with regenerated tarsi was not significantly different from that of normal insects. Likewise the duration of nymphal development for nymphs reared in groups was not appreciably different from that of nymphs reared separately, except for individuals that moulted seven times.

TABLE VII

NYMPHAL DEVELOPMENT IN *Periplaneta fuliginosa*

Instar	Duration in Days[a] of Each Instar and Nymphal Stage of Insects Reared Alone							
	Females			Males				
	Regenerated	N[b]		Normal	N[b]		Regenerated	N[b]
1	8.5 ± 0.3	8		9.7 ± 0.3	3		9.5 ± 0.5	8
2	17.8 ± 3.8	8		19 ± 8.9	3		26 ± 4.9	8
3	23 ± 5.2	8		34 ± 9.5	3		27 ± 4.8	8
4	48 ± 12	8		40 ± 8.7	3		34 ± 5.3	8
5	60 ± 12	8		41.3 ± 3.2	3		42 ± 4.7	8
6	53 ± 9.2	8		39 ± 8.0	3		42.4 ± 3.6	8
7	74 ± 13	8		33 ± 6.9	3		53 ± 7.1	8
8	54 ± 12	8		75 ± 12	3		102 ± 16	8
9	78 ± 13	8		141 ± 11	3		96 ± 22	8
10	96 ± 20	8		67	1		99 ± 19	6
11	92 ± 19	6		70	1		.....	.....
12	165	1		.....	.....		.....	.....
Nymphal Stage								
9 Moults				474 ± 16	2		494 ± 3.5	2
10 Moults	746 ± 138	2		.....	.....		509 ± 21	6
11 Moults	528 ± 54	5		586	1		.....	.....
12 Moults	681	1		.....	.....		.....	.....

DURATION IN DAYS[a] OF NYMPHAL DEVELOPMENT OF INSECTS REARED IN GROUPS

Females	N[b]	Males	N[b]
191 ± 28	8	179 ± 13	9

[a]Mean ± standard error.
[b]Number of insects.

Formation of the oötheca required about 24 hours. Females rotated their oöthecae with the keel either to the left or right, but mostly to the right. A few females retained oöthecae with the keel dorsal or only slightly tilted. Among mated females the number of eggs and the number that hatched per oötheca decreased with each successive oötheca after the third (fig. 1).

The longevity of adults of *Blattella vaga* is given in table X. There is a positive correlation between the number of cöthecae produced and the longevity of the female, both among females kept with males and among virgin females.

GROUP III

Blaberus craniifer.—Data on reproduction are given in table XIII. These observations were made early in the year when the temperature could be maintained at about 30° C.; the humidity was uncontrolled. The longevity of adults is given in table XIV. Data on nymphal development are given in table XV. These observations, up through the ninth instar, were made at a temperature of 30°–36° C. From the ninth moult

TABLE VIII

NYMPHAL DEVELOPMENT IN *Supella supellectilium*

INSTAR	DURATION IN DAYS[a] OF EACH INSTAR AND NYMPHAL STAGE OF INSECTS REARED ALONE							
	FEMALES				MALES			
	Normal	N[b]	Regenerated	N[b]	Normal	N[b]	Regenerated	N[b]
1	9.0±0.3	35	9.1±0.4	16	9.1±0.3	26	8.8±0.3	20
2	10.0±0.4	35	10.3±0.4	16	9.8±0.2	26	10.3±0.4	20
3	10.1±0.3	35	11.0±0.5	16	10.5±0.4	26	10.8±0.4	20
4	10.8±0.4	35	11.5±0.5	16	10.8±0.2	26	11.2±0.3	20
5	12.7±0.5	35	13.9±0.7	16	12.5±0.8	26	12.8±0.8	20
6	14.7±0.4	35	14.9±0.8	16	13.5±0.4	26	14.4±0.6	20
7	16.2±0.8	32	16.2±0.6	16	16.0±0.3	23	16.7±0.4	19
8	21.4±0.6	4	16.0±1.6	4				
NYMPHAL STAGE								
6 Moults	69.4±7.2	3			72.0±3.5	3	84	1
7 Moults	82.0±1.5	28	88.4±3.4	12	81.6±1.1	23	84.1±1.6	19
8 Moults	114.4±1.8	4	98.2±0.8	4				

DURATION IN DAYS[a] OF NYMPHAL DEVELOPMENT OF INSECTS REARED IN GROUPS

Females	N[b]	Males	N[b]
56.1±0.9	51	54.1±1.0	31

[a]Mean ± standard error.
[b]Number of insects.

TABLE IX

REPRODUCTIVE DATA FOR OVIPAROUS COCKROACHES THAT CARRY THEIR OOTHECAE EXTERNALLY UNTIL HATCHING

TYPE OF OBSERVATION	MEAN VALUES ± STANDARD ERROR					
	Blattella germanica		*Blattella vaga*			
	Mated Females[a]	N[b]	Mated Females[a]	N[b]	Virgin Females	N[b]
Oothecae per Female	6.6±0.5	9	5.5±0.4	25	3.3±0.4	24
Preoviposition Period, Days	7.8±0.3	9	7.9±0.2	25	9.7±0.4	24
Interval between Successive Oothecae, Days	22.0±0.3	50	24.2±0.4	112	22.4±1.3	54
Incubation Period, Days	17.2±0.1	48	19.8±0.1	84		
Period Females Carried Oothecae in which Eggs did not Hatch, Days	16.9±1.5	8	20.0±0.3[d]	38	20.1±0.2[e]	33
Eggs per Ootheca	36.7±0.9	56	27.7±0.7	122	21.0±0.6	38
Eggs Hatched Per Ootheca	27.8±2.2	55	19.1±1.3	122	0	38
Eggs Developed Parthenogenetically					3[f]	38
Percentage of Hatched Insects that Matured	85%	470	73%	247		
Sex Ratio[c] ♀♀:♂♂	1.12:1	309	1:1.09	245		

[a]Females kept with males and presumed mated.
[b]Number of insects or oothecae.
[c]Based on only those insects that matured.
[d]This figure does not include data from 5 oothecae that were carried for one day or less.
[e]This figure does not include data from 39 oothecae that were carried for one day or less.
[f]These eggs were all in the same ootheca.

to maturity the insects were kept at 19°–24° C. The humidity was uncontrolled. Half of the males with regenerated tarsi moulted one more time than normal insects.

Byrsotria fumigata.—Limited data on reproduction and nymphal development are given in table III. The data for nymphal development are for individuals from a single litter reared in a group; males matured more rapidly than females. These insects were maintained at 24° C. and 50–60% relative humidity.

Diploptera punctata.—All observations on reproduction except those on the seven females noted below were made at 24° and 50–60% relative humidity.

Reproductive data for this species are given in table XIII. The intervals between successive broods from seven females reared at a lower average temperature (19°–24° C.) were not essentially different from the values in the table, except that the interval between emergence and the hatch of the first brood was 146±7.3 days (N = 7)

TABLE X

LONGEVITY OF ADULT OVIPAROUS COCKROACHES AND ITS RELATION TO THEIR FECUNDITY

SPECIES	MEAN NUMBER OF DAYS ± STANDARD ERROR			
	FROM FORMATION OF LAST OÖTHECA UNTIL DEATH		ADULT LIFESPAN	
	Females	N*	Females	N*
Blattella germanica				
All specimens			153± 9	9
♀♀ producing the following number of oöthecae:				
0			140± 1	2
4	19	1	97	1
6	32±12	2	150±10	2
7	34± 8	3	173± 6	3
8	17	1	180	1
Blattella vaga				
♀♀ kept with ♂♂				
All specimens			150±12	22
♀♀ producing the following number of oöthecae:				
1	32	1	42	1
2	15	1	49	1
3	13± 8	2	68± 7	2
4	24± 3	2	99± 9	2
5	48±10	6	161±12	6
6	28± 8	3	157± 6	3
7	47± 7	5	196±10	5
8	52±14	2	225±19	2
Virgin ♀♀				
All specimens			108±10	23
♀♀ producing the following number of oöthecae:				
1	84±36	3	94±34	3
2	50±18	6	88±20	6
3	25±17	2	68±24	2
4	34±12	7	106±13	7
5	66±15	2	158±22	2
6	34± 3	2	174± 8	2
7	67	1	145	1
Periplaneta brunnea			241±59	2
			293±4.9	1
Supella supellectilium				
All specimens			90±2.9	35
			115±4.7	30
♀♀ producing the following number of oöthecae:				
5	53	1	141	1
7 to 8	19.6±1.1	5	70±2.7	5
9 to 10	23 ±5	11	92±4.7	11
11 to 12	12 ±3.1	7	84±2.4	7
13 to 14	10 ±2.1	7	91±3.8	7
15	19 ±4.3	3	102±6	3
18	10	1	121	1

*N = number of insects.

TABLE XI

NYMPHAL DEVELOPMENT IN *Blattella germanica*

INSTAR	DURATION IN DAYS[a] OF EACH INSTAR AND NYMPHAL STAGE OF INSECTS REARED ALONE							
	FEMALES				MALES			
	Normal	N[b]	Regenerated	N[b]	Normal	N[b]	Regenerated	N[b]
1	5.8±0.06	56	5.5±0.5	2	5.6±0.1	47	6.2±0.3	4
2	5.2±0.1	56	5.0±1.0	2	5.5±0.2	47	5.2±0.3	4
3	6.4±0.1	56	6.0±0.0	2	6.4±0.1	47	6.8±0.6	4
4	7.7±0.1	56	8.0±0.0	2	7.6±0.3	47	9.2±1.0	4
5	9.0±0.3	56	11.0±0.0	2	10.8±0.5	47	10.5±1.5	4
6	11.0±0.2	56	10.5±0.5	2	11.9±0.4	40	13.2±0.3	4
7	12.8±1.5	5			14	1		
NYMPHAL STAGE								
5 Moults					37.6±0.6	7		
6 Moults	44.6±0.5	51	46.0±1.0	2	47.2±1.0	39	51.2±3.2	4
7 Moults	62.6±1.4	5			52	1		

DURATION IN DAYS[a] OF NYMPHAL DEVELOPMENT OF INSECTS REARED IN GROUPS

Females	N[b]	Males	N[b]
41.3±0.5	153	40.1±0.6	137

[a]Mean ± standard error.
[b]Number of insects.

TABLE XII

NYMPHAL DEVELOPMENT IN *Blattella vaga*

INSTAR	DURATION IN DAYS[a] OF EACH INSTAR AND NYMPHAL STAGE OF INSECTS REARED ALONE							
	FEMALES				MALES			
	Normal	N[b]	Regenerated	N[b]	Normal	N[b]	Regenerated	N[b]
1	7.4±0.2	50	7.3±0.4	14	7.6±0.2	48	6.8±0.2	13
2	6.4±0.1	50	6.2±0.2	14	6.4±0.1	48	6.3±0.1	13
3	7.1±0.2	50	6.6±0.3	14	7.6±0.3	48	7.2±0.4	13
4	7.4±0.3	50	7.8±0.5	14	8.5±0.4	48	8.5±1.0	13
5	9.4±0.6	50	10.0±2.2	14	12.6±1.0	48	9.5±1.6	13
6	12.2±1.4	50	12.2±3.0	13	16.4±2.4	35	15.7±3.4	11
7	15 ±4.2	13	26 ±17	2	18 ±6.2	15	18 ±6.7	3
NYMPHAL STAGE								
5 Moults			33	1	35.8±0.8	13	33.5±1.5	2
6 Moults	43.0±0.7	37	43.5±1.2	11	51.2±3.2	20	43.4±1.7	8
7 Moults	84 ±8.3	13	116 ±42	2	93 ±9.2	15	103.3±1.2	3

DURATION IN DAYS[a] OF NYMPHAL DEVELOPMENT OF INSECTS REARED IN GROUPS

Females	N[b]	Males	N[b]
41.5±2.4	76	55.6±3.7	90

[a]Mean ± standard error.
[b]Number of insects.

as compared to 78.4±0.6 days (N=71), a highly significant difference. This period covered the coldest winter months and the lower temperature may have increased developmental time. Other reproductive data from the seven females maintained at 19°–24° C. fell into line with that of the larger group maintained at a constant temperature.

The incubation period was estimated because of the difficulty in finding females in the act of transferring the very small oötheca into the brood sac. Females of this species mate at emergence while still teneral (Roth and Willis, 1955a). By subtracting the period between broods produced and the interval from the hatch of the last brood until death.

Data on nymphal development are given in table XVI. Observations on nymphal development were made at a temperature of about 30° C. with occasional periods at 30°–36° C. Nymphs of this species moult fewer times than any other cockroach of which we know. Females usually undergo one more moult than the males and require a longer period to mature.

Leucophaea maderae.—All observations except those on virgin females were made at temperatures of about 30° C. with occasional periods at 36° C. The humidity was uncontrolled. Virgin females

TABLE XIII

COMPARATIVE REPRODUCTIVE DATA FROM COCKROACHES THAT CARRY THEIR OOTHECAE INTERNALLY UNTIL HATCHING

TYPE OF OBSERVATION	MEAN VALUES ± STANDARD ERRORS									
	Blaberus craniifer	N[b]	*Diploptera punctata*	N[b]	*Leucophaea maderae*	N[b]	*Nauphoeta cinerea*	N[b]	*Pycnoscelus surinamensis*[a]	N[b]
Broods per Female			3.0±0.1	78			6.2±0.3	16	3.4±1.1	20
Preoviposition Period, Days					19.8±2.0	5	13.4±2.6	5	7.3±0.3	3
Intervals between Hatches of Successive Broods, Days,										
Emergence to										
1st brood			78.4±0.6	71			44.1±0.9	11	41.6±0.3	20
1st to 2nd			72.4±1.2	67			40.1±0.9	13	48.1±2.2	28
2nd to 3rd			73.1±1.4	50			40.4±1.0	14	69.1±3.0	25
3rd to 4th			95 ±5.3	18			44.1±1.1	14	82 ±7.6	14
4th to 5th			97.5±3.5	2			46.9±3.9	13	75 ±4.4	5
5th to 6th							55 ±4.4	12		
6th to 7th							62 ±8.1	5		
7th to 8th							98.5±2.6	2		
Incubation Period, Days			66–70[c]		38 ±4	2	35.5±1.3	12	35.2±0.9	4
Eggs per Oötheca	34.3±3.3	18			33.8±1.2	28	32.8±0.5	55	26.4±2.4	13
Eggs Hatched per Oötheca	20.2±2.7	18	9.8±0.2	161	18.3±1.9	19	31.1±0.7	56	20.7±1.3[d]	20
Developed, Unhatched Eggs per Oötheca	3.2±0.6	18					1.0±0.4	56		
Undeveloped Eggs per Oötheca	10.7±1.8	18					0.6±0.2	56		
Percentage of Hatched insects that Matured	55%	42	90%	42	99%	143	99%	234	86%	141
Sex Ratio[e] ♀♀:♂♂	1:1.56	23	1.24:1	38	1:1.15	142	1.13:1	232	1:0	122

[a]Parthenogenetic strain that produces only females.
[b]Number of insects or oöthecae (broods).
[c]Based on only those insects that matured.
[d]First brood only.
[e]See text for explanation of this estimated value.

mating (or emergence) and appearance of an oötheca in the brood sac, about 8 to 12 days (Stay and Roth, 1958), from the known interval between emergence and hatch of the first brood, we estimated the incubation period to be 66–70 days. The estimated value of 50 days for embryogenesis that we had previously cited (Riser in Roth and Willis, 1955a) was based on one observation.

Longevity of adults of *Diploptera punctata* is given in table XIV. There is a positive correlation between the longevity of the female and the number of broods she produced. There is a negative correlation between the number of

were maintained at 24° C. and 50–60% relative humidity.

Five days after emergence as adults, males courted females of the same age, but the youngest females seen in copulo were eleven days old. In the late afternoon males were frequently seen performing the courting actions described by Roth and Willis (1954).

Reproductive data from mated females are given in table XIII. The oöthecae from 18 virgin females were examined when they were aborted. No evidence of parthenogenetic development was found. Six of the females lived an average of 159±31 days; 12 were alive when the

experiment was stopped and had been observed for an average of 363 ± 18 days.

Data on nymphal development are given in table XVII. Females usually undergo one more moult than the males and take longer to mature. Nymphs can climb glass at birth.

Nauphoeta cinerea.—Nymphal development was observed at temperatures close to 30° C. Data on reproduction was obtained at this temperature during most of the year, but in summer there were occasional periods when the temperature reached 36° C. The humidity was uncontrolled.

In this species copulation occurred as early as six days after the adults had emerged. Males assumed the courting position, with wings elevated, five days after emergence and would remain in this pose for several minutes in the presence of females. The longevity of the adults is given in table XIV.

Egg production, as determined by the number of nymphs that hatched, increased with each oötheca up to the third but fell off with the formation of successive oöthecae thereafter. This relationship is shown in figure 1. Concurrently the intervals between broods increased with successive oöthecae after the third. This relationship is shown and other reproductive data are given in table XIII. The data on egg production in *N. cinerea* that are given in table XIII were from different females than those used to obtain the curve in figure 1. The sequence of formation was not known for the oöthecae used to obtain the data for the table.

Hatching of the nymphs, as the female extrudes the oötheca from her brood sac, has been described for two females of this species by Roth and Willis (1954). Over 100 additional observations of birth in *Nauphoeta cinerea* confirmed this mode of hatching. The nymphs shed their embryonic membranes as they hatch and subsequently eat

TABLE XIV

LONGEVITY OF ADULT COCKROACHES THAT CARRY THEIR OÖTHECAE INTERNALLY AND ITS RELATION TO THEIR FECUNDITY

SPECIES	MEAN NUMBER OF DAYS ± STANDARD ERROR					
	FROM HATCH OF LAST BROOD UNTIL DEATH		ADULT LIFESPAN			
	Females	N*	Females	N*	Males	N*
Blaberus craniifer			475 ± 88	8	425 ± 67	10
Diploptera punctata						
All specimens			355 ± 13	78	442 ± 25	5
♀♀ producing the following number of broods:						
1	144 ± 48	1	226 ± 47	4		
2	118 ± 31	19	284 ± 32	19		
3	135 ± 24	33	359 ± 16	33		
4	104 ± 17	18	423 ± 17	18		
5	58 ± 20	4	490 ± 13	4		
Nauphoeta cinerea						
All specimens			344 ± 16	16	365 ± 14	16
♀♀ producing the following number of broods:						
3			412	1		
4	18	1	224	1		
5	43	1	257	1		
6	41 ± 12	5	332 ± 10	5		
7	53 ± 7	6	362 ± 23	6		
8	38 ± 6	2	388 ± 74	2		
Pycnoscelus surinamensis[b]						
All specimens			307 ± 17	29		
♀♀ producing the following number of broods:						
0			290	1		
1	3	1	180	1		
2	199 ± 105	3	279 ± 106	3		
3	137 ± 27	10	294 ± 27	10		
4	73 ± 27	9	305 ± 27	9		
5	65 ± 19	5	385 ± 19	5		

*Number of insects.
[b]Parthenogenetic strain.

both membranes and oötheca. Older nymphs and adults would also eat the shed embryonic membranes and oötheca. Occasionally they would attempt to eat the oötheca and the hatching nymphs, as the female ejected the oötheca, even to the extent of pulling the oötheca away from the mother. Some females would turn their abdomens away from the attack as though to protect the hatching nymphs. Recently hatched nymphs crawled beneath the female, even under her wings, and remained there for about an hour after hatching. Presumably the nymphs might also take shelter under other available objects. The nymphs can climb glass at birth.

Data on nymphal development are given in table XVIII. Both sexes moult the same number of times and the females take a longer time to mature than the males. Nymphs reared in groups matured somewhat more rapidly than those reared separately. Incidental to certain behavior studies with this species, 13 nymphs which had been starved for the first 16 days fol-

TABLE XV

NYMPHAL DEVELOPMENT IN *Blaberus craniifer*

INSTAR	DURATION IN DAYS[a] OF EACH INSTAR AND NYMPHAL STAGE OF INSECTS REARED ALONE					
	FEMALES		MALES			
	Normal	N[b]	Normal	N[b]	Regenerated	N[b]
1	14.9± 0.5	9	16.6±1.7	8	15.5± 0.4	6
2	18.0± 0.6	9	18.9±1.1	8	23 ± 4.2	6
3	16.5± 0.4	9	18.0±0.9	8	22.8± 3.4	6
4	17.7± 0.8	9	19.2±1.2	8	19.5± 1.4	6
5	21.9± 1.0	9	24.8±2.2	8	22.2± 1.0	6
6	23.6± 1.3	9	21.1±0.6	8	23.2± 1.0	6
7	22.8± 1.3	9	23.4±1.4	8	20.7± 1.1	6
8	22.4± 0.8	9	23.8±2.3	8	21.2± 0.5	6
9	37.9± 2.8	9	31.6±1.4	8	28.2± 2.6	6
10	81 ±20	9	59.6±3.4	8	50 ± 6.8	6
11	.....		.....		80 ±14	3
NYMPHAL STAGE						
10 Moults	273 ±18	9	257 ±5.9	8	241 ± 8.7	3
11 Moults	.....		.....		332 ±47	3

[a]Mean ± standard error.
[b]Number of insects

TABLE XVI

NYMPHAL DEVELOPMENT IN *Diploptera punctata*

INSTAR	DURATION IN DAYS[a] OF EACH INSTAR AND NYMPHAL STAGE OF INSECTS REARED ALONE							
	FEMALES.				MALES			
	Normal	N[b]	Regenerated	N[b]	Normal	N[b]	Regenerated	N[b]
1	9.3±0.2	16	8	1	9.6±0.3	8	9.3±0.7	3
2	9.9±0.2	16	10	1	10.9±0.3	8	12.3±0.4	3
3	14.3±0.7	16	14	1	16.2±0.6	8	18.0±0.0	3
4	19.1±0.6	15	16	1	18	1	19	1
NYMPHAL STAGE								
3 Moults	43.	1	.....		37.7±0.5	7	39.0±1.0	3
4 Moults	52.1±1.1	15	48	1	48	1	60	1

DURATION IN DAYS[a] OF NYMPHAL DEVELOPMENT OF INSECTS REARED IN GROUPS

Females	N[b]	Males	N[b]
51.2±0.5	4	41.5±1.8	6

[a]Mean ± standard error.
[b]Number of insects.

TABLE XVII

NYMPHAL DEVELOPMENT IN *Leucophaea maderae*

INSTAR	DURATION IN DAYS[a] OF EACH INSTAR AND NYMPHAL STAGE OF INSECTS REARED ALONE							
	FEMALES				MALES			
	Normal	N[b]	Regenerated	N[b]	Normal	N[b]	Regenerated	N[b]
1	13.3±0.5	11	12.8±0.6	11	12.3±0.2	26	11.8±0.3	12
2	12.7±0.3	11	13.2±0.6	11	11.5±0.3	26	13.7±0.7	12
3	15.5±0.7	11	16.5±0.7	11	15.7±0.5	26	18.2±1.3	12
4	19.6±1.0	11	19.2±0.7	11	17.5±0.8	26	19.5±1.5	12
5	20.8±0.9	11	18.7±0.8	11	19.4±0.7	26	19.4±1.1	12
6	23.6±0.9	11	22.3±1.1	11	23.1±0.8	26	21.6±0.9	12
7	26.1±1.3	11	23.6±1.0	11	27.9±0.4	26	26.7±1.2	12
8	31.3±1.4	11	29.7±0.7	11	.....		29.2±0.6	5
NYMPHAL STAGE								
7 Moults	131 ±4.2	3	.....		127 ±2.4	26	126 ±1.6	7
8 Moults	163 ±3.4	11	156 ±3.8	11	.....		167 ±6.2	5

DURATION IN DAYS[a] OF NYMPHAL DEVELOPMENT OF INSECTS REARED IN GROUPS

Females	N[b]	Males	N[b]
150±2.7	41	121±2.0	38

[a]Mean ± standard error.
[b]Number of insects.

TABLE XVIII

NYMPHAL DEVELOPMENT IN *Nauphoeta cinerea*

INSTAR	DURATION IN DAYS[a] OF EACH INSTAR AND NYMPHAL STAGE OF INSECTS REARED ALONE							
	FEMALES						MALES	
	NORMAL							
	Biparental	N[b]	Parthenogenetic[c]	N[b]	Regenerated	N[b]	Normal	N[b]
1	10.2±0.2	26	14.0±1.5	3	11.8±1.6	5	9.1±0.4	20
2	8.8±0.2	26	9.0±0.6	3	9.0±0.3	5	8.4±0.2	20
3	8.4±0.2	26	9.3±0.4	3	8.0±0.4	5	8.0±0.2	20
4	9.5±0.2	26	10.7±0.3	3	10.0±0.6	5	8.6±0.1	20
5	10.3±0.2	26	11.0±0.6	3	10.2±0.7	5	9.7±0.2	20
6	12.3±0.5	26	11.7±0.7	3	13.8±1.6	5	11.0±0.3	20
7	15.5±0.5	26	14.3±0.3	3	13.6±0.4	5	15.2±0.6	20
8	20.4±0.2	21	18.3±0.4	3	18.0±1.8	5	18.9±0.3	11
9	.....		.....		22.5±0.5	2	.....	
NYMPHAL STAGE								
7 Moults	79.8±0.3	5					72.8±0.9	9
8 Moults	94.2±0.9	21	98 ±3.5	3	96 ±3.5	3	86.6±0.9	11
9 Moults	.....		.....		114 ±2.5	2	.....	

DURATION IN DAYS[a] OF NYMPHAL DEVELOPMENT OF INSECTS REARED IN GROUPS

Females	N[b]	Males	N[b]
85.4±1.2	100	71.6±0.3	88

[a]Mean ± standard error.
[b]Number of insects.
[c]Offspring of an unmated female.

lowing hatching were later fed continuously; these starved nymphs were delayed approximately 16 days (the period of starvation) in attaining the first and last moults.

Pycnoscelus surinamensis.—Nymphal development was observed at about 30° C. Observations on reproduction were started at this temperature, but after the females had formed the second oötheca the insects were removed to temperatures that ranged from 19°–24° C. The humidity was uncontrolled.

TABLE XIX

NYMPHAL DEVELOPMENT IN *Pycnoscelus surinamensis*, PARTHENOGENETIC STRAIN, ALL FEMALES

INSTAR	DURATION IN DAYS[a] OF EACH INSTAR AND NYMPHAL STAGE OF INSECTS REARED ALONE			
	Normal	N[b]	Regenerated	N[b]
1	15.2±1.0	37	15.7±0.9	24
2	14.6±0.5	37	17.2±1.5	24
3	12.9±0.6	37	12.6±0.4	24
4	12.0±0.3	37	12.1±0.3	24
5	12.5±0.2	37	13.0±0.3	24
6	13.0±0.2	37	12.7±0.2	24
7	14.2±0.3	37	13.9±0.4	24
8 (not last instar)	16.5±0.5	28	15.7±1.3	23
8 (last instar)	35.0±2.7	9	52	1
9 (not last instar)	16.6±0.9	5	19.6±0.4	6
9 (last instar)	45.6±2.9	23	44.1±1.9	17
10 (last instar)	49 ±7.4	5	42 ±5.9	6
11 (not last instar)	.....		18	1
12 (last instar)	.....		27	1
Nymphal Stage				
8 Moults	127 ±2.1	9	149	1
9 Moults	156 ±3.2	23	153 ±1.9	17
10 Moults	184 ±5.1	5	186 ±9.8	5
12 Moults	.....		205	1

DURATION IN DAYS[a] OF NYMPHAL DEVELOPMENT OF INSECTS REARED IN GROUPS

140 ±2.1 61

[a]Mean ± standard error. [b]Number of insects.

Data on reproduction in this species are given in table XIII. Only the number of eggs that hatched from the first formed oötheca are given. The insects were moved from the laboratory while the second oötheca was in the brood sac. This move apparently induced most of the females to abort their oöthecae before the embryos had completed development. Hatching of the second and succeeding oöthecae was very erratic and obviously not normal.

The intervals between hatching of successive broods increased progressively as the females aged. This is thought not to be associated with the lower ambient temperatures that prevailed during the latter part of the experiment because the time increased gradually from brood to brood, whereas the temperature change was discontinuous. The longevity of adult females and its relation to the number of broods produced are given in table XIV.

Data on nymphal development are given in table XIX. In this species the eighth and ninth instars were shorter when they were penultimate than when they were the last instar. For this reason two values are given in the table for each of these instars. No such phenomenon was observed in any of the other species. Nymphs of this species are unable to climb glass until the fifth instar.

SUMMARY

Observations on reproduction and development in seventeen species of cockroaches are presented in tabular form. The cockroaches studied represent three types of oviposition behavior (1) oviparous species that drop their oöthecae shortly after formation: *Blatta orientalis, Cariblatta lutea minima, Eurycotis floridana, Neostylopyga rhombifolia, Periplaneta americana, P. australasiae, P. brunnea, P. fuliginosa,* and *Supella supellectilium*; (2) oviparous species that carry their oöthecae externally until, or shortly before hatching: *Blattella germanica* and *B. vaga*; (3) species which carry their oöthecae in a brood sac until hatching: false ovoviviparous species, *Blaberus craniifer, Byrsotria fumigata, Leucophaea maderae, Nauphoeta cinerea, Pycnoscelus surinameusis,* and the false viviparous species, *Diploptera punctata.*

Parthenogenesis was found in the following species in which it has not been reported previously: *B. vaga, E. floridana, N. rhombifolia, P. australasiae,* and *P. brunnea.* Unfertilized eggs of only *E. floridana* and *P. brunnea* hatched. Only parthenotes of *P. brunnea* completed nymphal development; all were females. Parthenogenesis has also been reported for *P. americana* (Roth and Willis, 1956); of the three species of *Periplaneta* in which parthenogenesis has been observed, virgin females of *P. australasiae* have performed most poorly. Parthenogenesis was not found in *L. maderae* that were observed for over a year.

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NEW SPECIES BELONGING TO THE GENERA AMBLYSEIUS AND AMBLYSEIOPSIS WITH KEYS TO AMBLYSEIUS, AMBLYSEIOPSIS, AND PHYTOSEIULUS[1]

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Several genera of Phytoseiidae are known from the United States. All or most of them are predators of Tetranychidae (spider mites), Eriophyidae, (gall mites), Tarsonemidae or related groups. A few are plant feeders. The genera studied are closely related to *Typhlodromus* (*Seius, Seiulus, Iphidulus*) but differ chiefly in the comparative length of dorsal, lateral and leg setae.

Retention of *Amblyseiopsis* has been considered carefully. The array of structural differences given in the key seems to justify separation from *Amblyseius* in spite of the opinion of certain authors who combine them. *Amblyseiopsis* in many respects approaches *Typhlodromus* more closely than *Amblyseius*. The trend to elongate lateral setae is carried over into the genus *Phytoseiulus*, but that genus possesses a characteristic anal plate which is more remote from the genital plate than in any representative of *Amblyseiopsis* or *Typhlodromus* that we have. It would tend to fall in *Garmania* as diagnosed by Nesbitt, except for the chaetotaxy of the dorsum. Muma placed

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Dr. M. H. Muma supplied species represented in his Florida descriptions which have been helpful and much appreciated.

his "setosa" in a new genus *Amblysiella*, but except for the length of one pair of dorsal setae it seems to correspond throughout with *Phytoseiulus*.

Only species of *Amblyseius*, *Amblyseiopsis*, and *Phytoseiulus* are considered in this paper.

KEY TO DESCRIBED AND RELATED GENERA

1. Sternal plate usually much shorter than wide.[3] Anal plate of female slightly shorter than wide. Peritreme plate heavily chitinized, usually sharply truncate, the chitinized portion extending as far forward as Leg I; whole body heavily chitinized ..... **Amblyseius**
— Sternal plate either longer than wide or close to the same width. Anal plate of the female longer than wide. Peritreme plate not heavily chitinized as far forward as Leg I, or sharply truncate. Body weakly chitinized 2
2. Anal plate not remote from the genital, either close or in contact with it. Six pre-anal setae and 2 pores in addition. Dorsal setae never conspicuously elongate 3
— Anal plate remote from the genital. Dorsal setae sometimes elongate 4
3. Marginal and some of the leg setae elongate, much longer than the dorsal. Anal plate with 6 pre-anals (3 pairs) and 2 pores ..... **Amblyseiopsis**
— Marginal and leg setae not conspicuously longer than the dorsal setae. Anal plate frequently with 8 pre-anals (4 pairs) and 2 pores ..... **Typhlodromus**
4. Setae of dorsal plate numerous; more than two median ..... **Garmania**
— Setae of the dorsal plate few, some occasionally elongate ..... **Phytoseiulus**

Descriptions have been standardized and kept as brief as possible. Generic characters are not repeated for the most part in specific descriptions. Measurements of body size refer only to the idiosoma excluding the gnathosoma, and including propodosoma, metapodosoma and opisthosoma.

KEYS TO SPECIES

Amblyseius

1. Accessory parapodals circular or slightly oval; at least 4 elongate lateral setae on each side of dorsum ..... **grandis**
— Accessory parapodals elongate; only 2 elongate lateral setae on each side ..... **quadripilis**

Phytoseiulus

1. Dorsal setae 5 as long or longer than L 4; pre-anal setae in antero-lateral corners, pores mesad. Para-anals in front of anal plate ..... **macropilis**
— Dorsal setae 5 shorter than L 4; pre-anal setae almost half way between front margin and anal opening, pores almost in line longitudinally. Para-anals in usual position alongside of anal plate ..... **setosa**

Amblyseiopsis

1. Pores of the anal plate slit or crescent shaped 2
— Pores of the anal plate circular, sometimes minute 5
2. Pores and setae of the anal plate grouped in the anterior-lateral corners ..... **limonicus**
Pores and setae of the anal plate not grouped in the anterior-lateral corners 3
3. Caudal margin of the sternal plate recessed as in Fig. 9,a ..... **potentillae**
— Caudal margin of the sternal plate not recessed 4
4. Pores of the anal plate very close to the posterior pre-anal setae. Accessory parapodals very slender, Fig. 9,c ..... **largoensis**
— Pores of the anal plate more remote rom the posterior pre-anal setae. Accessory parapodals wider Fig. 7,c ..... **aeralis**
5. Pores of the anal plate almost as far forward as the posterior pre-anal setae 6
— Pores of the anal plate much further to the rear, frequently, longitudinally in line with the posterior pre-anals 9
6. Anal plate narrower than the genital ..... **sexta**
— Anal plate as wide or wider than the genital 7
7. Posterior lateral setae longer than the body width ..... **musae**
— Posterior laterals[4] shorter than the body width 8
8. Anal plate emarginate at sides ..... **tropicanus**
— Anal plate not emarginate at sides ..... **mexicanus**
9. More than five long lateral setae 10
— Five long lateral setae or less 11
10. Six long laterals ..... **reticulatus**
— Seven long laterals ..... **septa**
11. Accessory parapodals elongate 12
— Accessory parapodals short, almost semicircular Fig. 16,c 15
12. Pre-anal pores almost as far forward as the posterior pre-anal setae. Five long lateral setae ..... **ovatus**
— Pre-anal pores much behind the posterior pre-anals. Four long laterals 13
13. Anal plate of the same width as the genital ..... **americanus**
— Anal plate wider than the genital 14
14. Teeth of the chelicerae short ..... **oregonensis**
— Teeth of the chelicerae large and coarse, moveable arm ⅔ as long as the fixed ..... **floridanus**
15. Anal plate wider than the genital. Accessory parapodals parallel to the primaries and not cephalad of the latter ..... **gracilis**
— Anal plate nearly the same width as the genital. Accessory parapodals in front of a transverse line through the front of the primaries. **elongatus**

Amblyseius grandis Berlese

(Fig. 1), (2, 1914)[5]

Female. Lateral setae 1, 4, 6, and 8 much longer than the others. Chelicerae with 4 teeth on fixed arm. Legs with longer setae on tibia genual and first tarsal segments of leg IV. Sternal plate with 3 setae each side nearly equally separated. Anal plate much wider than the genital, reticulate and with 3 pairs setae besides the para anals, and 1 pair of pores. Anterior para anals nearly in line with the front margin of the anal opening. Peritreme plate heavily reinforced, squarely truncate at posterior end. Parapodals consisting of one thick elongate one and a nearly circular smaller one alongside. Parapodals and genital armature as in Fig. 1.

Male not available.

Measurements. *Female*. Length 0.44 to 0.47 mm., width 0.34 mm., Leg IV 0.44 mm.

Habitat. Apple bark, Connecticut. West Virginia, apple soil. Pennsylvania, Digitalis.

[3]Narrowest width by shortest length. *Amblyseius* often 2 to 4 times as wide as long, but there is some variation within species.

[4]Technically M_2 if the small seta alongside is a "lateral".

[5]See references.

Relationships. This species has a wide anal plate and a small accessory nearly circular parapodal plate, in which it differs from *quadripilis*.

Amblyseius quadripilis Banks

(Fig. 2) (4, 1905, *Seius*)

Female L4 and L8 long, dorsals very short, posterior dorsals lacking. Chelicerae with 8–10 prominent teeth on the fixed arm. Leg IV with elongate setae on genual, tibia and first tarsal segments decreasing in length in that order. Coxae each side practically in contact except the first two which are slightly separated. Sternal plate 2 to 3 times as wide as long. Anal plate not broader than the ventral or genital, 3 paired setae in anterior portion and 1 pore almost as far forward as the two lateral setae. Genital armature linear—not expanded. Parapodal plates conspicuous, a pair each side, smaller one nearly half as long as the larger. Metapodals elongate as in Fig. 2,a. Tracheae of the peritreme extending not quite to the front margin of Coxa I, not as far as D1 setae. Peritreme plate blunt at posterior end and distietly rounded. (Fig. 2,a).

Male not available.

Measurements. Female 0.420 by 0.330 mm., leg IV 0.390 mm. Posterior lateral seta 0.10 mm.

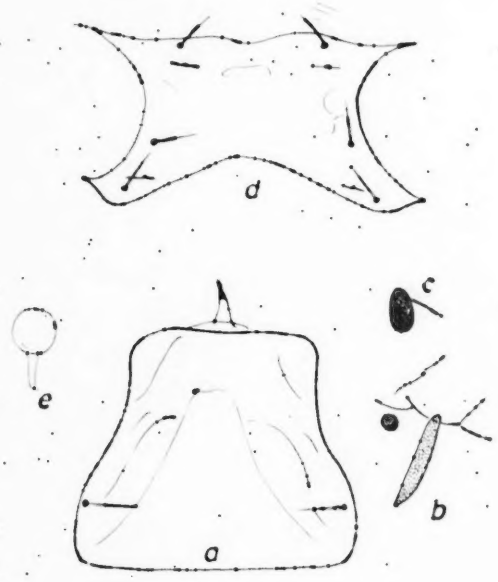

Fig. 1

Fig. 1.—*Amblyseius grandis* Berlese. a. genital plate, b. parapodal plates, c. metapodal plate, d. sternal plate, e. coxal gland. (Sternal plate figure is turned upside down.)

Habitat. Citrus, from Florida and Mexico.

Relationships. This heavily chitinized species is characterized by possession of only 4 long laterals, 2 on each side, arrangement of the parapodals, rounded blunt end of the peritreme plate and the pointed genital armature.

Phytoseiulus setosa (Muma) n. comb.

(7, 1955)

Female. Laterals all long, at least six of them very long. Chelicerae with only 3 teeth at tip of fixed arm. Leg IV with usual setae, that on tibia slightly shorter. Anal plate narrowed anteriorly, with only one pair of pre-anal setae. Two pores longitudinally in line with pre-anal setae. Parapodals long, slender, accessory parapodals indistinct or lacking. Tracheae extending to D1, peritreme plate bluntly rounded or truncate at posterior end.

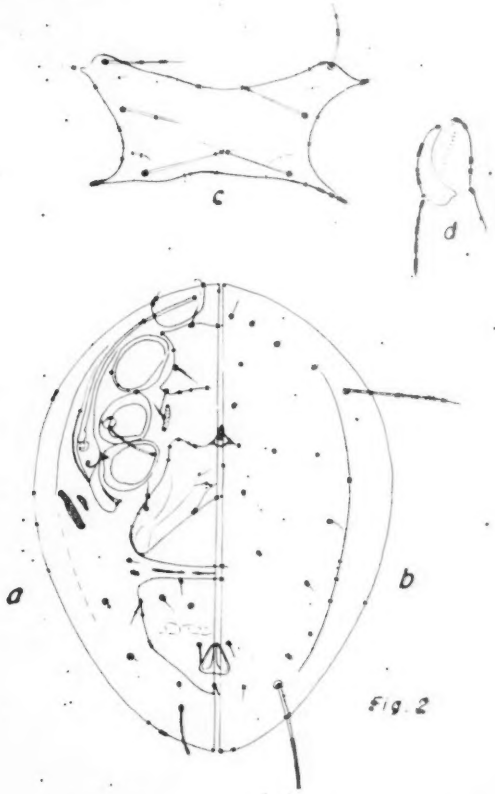

Fig. 2

Fig. 2.—*Amblyseius quadripilis* Banks. a. ventral surface, b. dorsal surface, c. sternal plate, d. chelicerae.

Male not available.

Measurements. Female 0.41 by 0.25 mm. Leg 0.10 0.05 mm. Leg IV 0.53 mm.

Male (Muma) 0.30 by 0.18 mm.

Habitat. (From Muma). Scaly orange leaves at Tampa, Fla. Grapefruit, Clearwater, Fla. Types in the U.S.N.M.

Relationships. Conspicuous by the presence of at least 6 long lateral setae and the presence of only one pair of pre-anal setae on the anal plate. Differs from *P. macropilis* in having D5 short. (See 3 p. 23, 1953). Originally placed in *Amblysiella* by Muma, but owing to the general similarity of structure, particularly the anal plate region, it is here transferred to *Phytoseiulus*.

Amblyseiopsis limonicus G.

(Fig. 3) (6, pl. 5)

Female. Dorsum with lateral setae 1, 4 and 9 longer than others though not as long as in other members of the genus. Dorsals very minute, two small scapulars; pores as in Figure 3. Chelicerae with 7 to 9 teeth on the fixed arm. Palpi each with a spatulate seta on the inside of segment 3. Leg IV with longer setae on genual, tibia and first tarsal segment. Anal plate (Fig. 3) expanded anteriorly with forward setae grouped somewhat as in *T. finlandicus*, but the spacing between the setae more unequal and the middle pair nearer the anterior margin. Two lunate pores as in Figure 3,a. Sternal plate with 3 setae each side. An almost circular metapodal plate behind the caudo-lateral angle on each side. Parapodal plates consisting of a slender pair on each side, almost needle-like, the smaller one about ⅕ as long as the larger. Peritreme plate blunt at the posterior end, but not as squarely truncate as in some members of the genus. Tracheae each side extending forward to D1. Genital armature semicircular in appearance with lines radiating from the anterior margin.

Male not available.

Measurements. Female. Length 0.198–0.240 mm., width 0.135 mm., leg IV 0.255–0.285 mm., posterior lateral seta 0.05–0.06 mm.

Habitat. Found on orange and lemon, California presumably feeding on Tetranychidae.

Holotype. Santa Ana Slide "Lot" 40–21386.

Notes. The anal plate of this species strongly resembles that of *Typhlodromus finlandicus*, but there is a noticeable difference in the spacing of the setae in relation to one another. There is also an important difference in the length of the tracheae which extend much farther forward than those of *finlandicus*. In addition, the chelicerae bear a conspicuous row of teeth not seen in *finlandicus*. The length of the lateral setae as mentioned above and the small size of the dorsals place it in *Amblyseiopsis*.

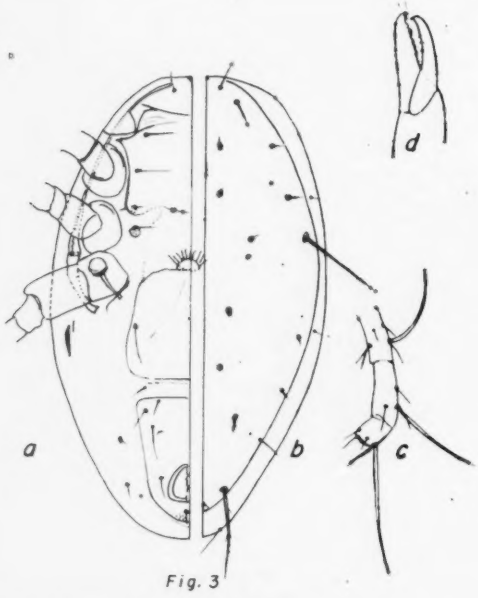

Fig. 3.—*Amblyseiopsis limonicus* n. sp. a. ventral surface, b. dorsal surface, c. leg IV, d. chelicerae.

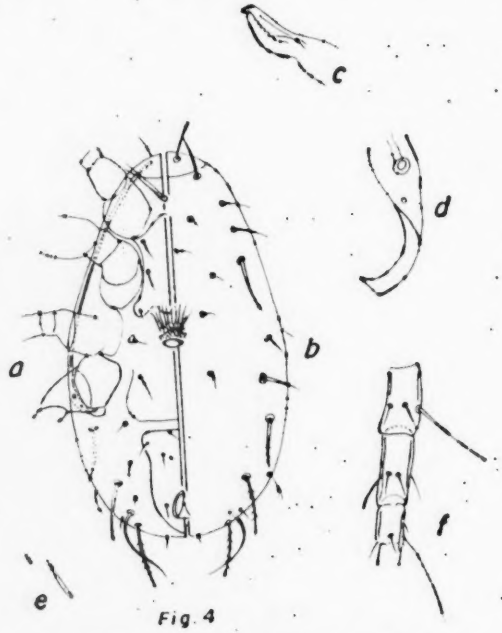

Fig. 4.—*Amblyseiopsis sexta* n. sp. a. ventral surface, b. dorsal surface, c. chelicerae, d. peritreme plate, e. parapodal plates, f. Leg IV setae.

Amblyseiopsis sexta n. sp.

(Fig. 4)

Female. Laterals 1, 2, 3, 4, 6, 7, 8, and 10 very thick, 8 with a tendency to plumosity.

Dorsals fairly short, but longer than in most *Amblyseius*. Fig. 4,b. Chelicerae with 6 large teeth on fixed arm, 2 smaller ones distad. Expanded seta on the third segment of the palpus, inside. Leg IV with enlarged seta on genual and first tarsal segment, that on tibia much shorter. Anal plate slightly expanded anteriorly, constricted at middle, with 3 pre-anal setae each side and an oval pore on each side close to the posterior. Para-anals slightly in front of the middle of the anal opening. Parapodals thick, short, accessories linear, short as in (Fig. 4,e). Tracheae of the peritreme extending forward to D1, plate obliquely truncate posteriorly. Genital armature of peculiar crown-like formation.

Male not available.

Dimensions. 0.318 to 0.360 by 0.15 to 19 mm. Leg IV 0.275–0.357, L8 0.06–0.1 mm.

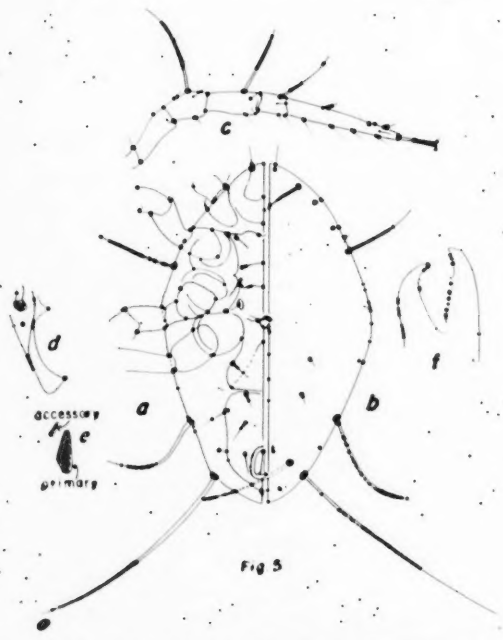

FIG. 5.—*Amblyseiopsis musae* n. sp. a. ventral surface, b. dorsal surface, c. Leg IV, d. peritreme plate, e. parapodal plates, f. chelicerae showing teeth.

Habitat. Brownsville, Texas, roses May 13, 14, 1936. Larkspur and fern May 10, 1936; crape myrtle Aug. 9, 1937; tuberoses Sept. 17, 1937; zinnias May 26, 1936; gardenia Feb. 5, 1937. Hildago, Texas, lettuce, Apr. 30, 1936.

Types. Types and paratypes slides nos. 36–23485 (type), 36–23470, 36–22518, 37–4065, 37–23461, 37–15604, 37–22586.

Relationships. Distinguished by the number and position of heavy lateral setae. Plumosity of L10, arrangement of the anal plate setae so far forward, size and shape of parapodal and the peculiar crown-like appearance of the genital armature of the female. A very weakly chitinized species, more elongate than others of the genus.

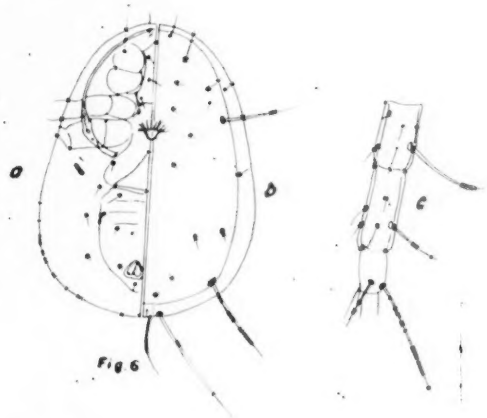

FIG. 6.—*Amblyseiopsis mexicanus* n. sp. a. ventral surface, b. dorsal surface, c. Leg IV.

Amblyseiopsis musae n. sp.

(FIG. 5)

Female. Lateral setae L 1, L 4, L 7, L 9 long, L 9 longer than the body width. Dorsals very minute. Seven to 10 teeth on the fixed arm of the chelicerae. Leg IV with long setae on genual tibia and first tarsal segments gradually decreasing in length in the order given. Genital armature inconspicuous, with inconspicuous lines radiating from the anterior margin. Anal plate with 6 pre-anal setae and one pair of pores close

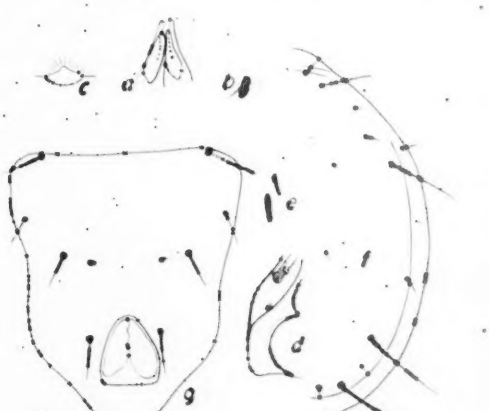

FIG. 7.—*Amblyseiopsis aeralis* Muma. a. chelicerae, b. metapodal plate, c. genital armature, d. peritreme plate, e. parapodal plates, f. dorsal setae, g. anal plate.

to the posterior. Para-anals in front of the middle of the anal opening. Parapodals elongate (cigar-shaped) Fig. 5,e, the smaller accessory plate more than half as long, very slender and placed at a distinct angle. Peritreme extending forward to seta D1.

Male. Unknown.

Dimensions. Female 0.36 by 0.23 mm., leg IV 0.36 mm. Posterior lateral setae 0.30–0.34 mm.

Habitat. On bananas, Haiti and Cuba.

Types. Slide 44040, U. S. National Museum collection.

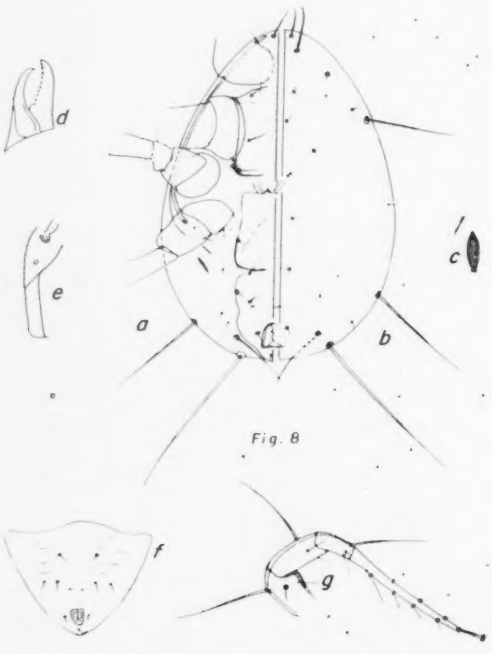

Fig. 8

FIG. 8.—*Amblyseiopsis largoensis* Muma. a. ventral surface, b. dorsal surface, c. parapodal plates, d. chelicerae, e. peritreme plate, f. anal plate, male, g. Leg IV.

Relationships. Characterized by extremely long lateral setae, the inconspicuous genital armature and the very small dorsal setae. Also by the lunate pores between the posterior pre-anal setae and the long accessory parapodals more than half as long as the primary and set at a distinct angle. Nearest relative *aeralis*.

Amblyseiopsis americanus Garman

(5) 1948.

Female. Four long lateral setae. Four to 7 teeth on the fixed arm of the chelicerae. Long setae on Leg IV genual, tibia and first tarsal segments, gradually declining in length in the order given. Three setae each side on the sternal plate equally spaced. Genital armature slight, pointed, inconspicuous. Anal plate with three pairs setae on each side besides the para-anals and minute pores behind the posterior pre-anal and almost as far laterad. Parapodals consist of a long cigar-shaped (somewhat triangular) plate and a smaller slender one alongside about one-half as long. Posterior end of peritreme plate truncate, tracheae extending forward to setae D1.

Male. Chelicerae with conspicuous T-shaped appendage.

Fig 9

FIG. 9.—*Amblyseiopsis potentillae* n. sp. a. sternal plate, b. peritreme plate, c. parapodal plates, d. genital armature, e. anal plate, f. dorsal surface.

Measurements. Female. Length 0.36–0.42 mm. width 0.19–0.28 mm., leg IV 0.34 mm., posterior lateral seta 0.19–0.23 mm.

Habitat. Apple bark and leaves, Connecticut. Types in possession of The Connecticut Agricultural Experiment Station.

Relationships. Position of pores on the anal plate (omitted in the original description), shape of the parapodals and the genital armature distinguish this species from others. None of the specimens in our collection is heavily chitinized. The nearest relative is *oregonensis* which is distinguished by a broader anal plate, longer L2 and L3 and a striate-reticulate anal plate.

Amblyseiopsis mexicanus n. sp.

(Fig. 6)

Female. Pattern of dorsal setae as in Fig. 6,b. L 4, 7, and 9 long. Chelicerae with 3–4 teeth on the fixed arm. Leg IV with the usual elongate setae on genual, tibia, and first tarsal segments. Sternal plate with 3 setae on each side almost equally spaced. Metapodals slightly oval, longer than broad. Parapodals cigar-shaped, smaller one of each pair about one-third as long as the larger. Anal plate as in Fig. 6, a. Trachea of peritreme extending between D1, posterior end of peritreme plate blunt but not truncate. Genital armature almost triangular to oval.

Male unknown.

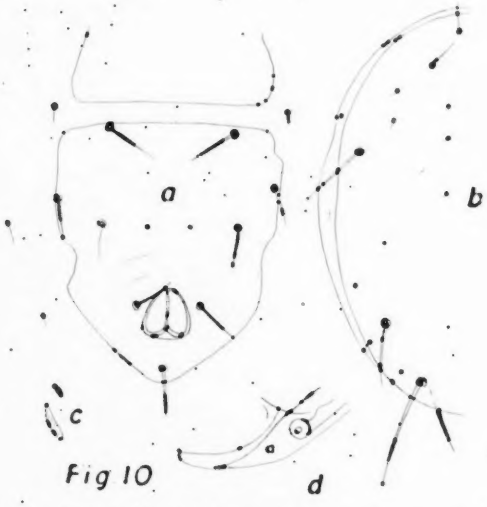

Fig 10

Fig. 10.—*Amblyseiopsis tropicanus* n. sp. a. anal plate, b. dorsal surface, c. parapodal plates, d. peritreme plate.

Measurements. 0.275 to 0.330 by 0.165 to 0.202 mm. Leg IV 0.330. Posterior lateral 0.12 mm.

Habitat. On zinnia, shasta daisies and chrysanthemum at Brownsville, Texas, intercepted from Mexico.

Types. Slide of June 27, 1937, from zinnia, lot 37-20191 G. E. Callaghan Colr. U. S. National Museum collection.

Relationships. This species is near to *americanus* but differs in certain details mentioned under *americanus*.

Amblyseiopsis aeralis Muma

(Fig. 7) (7, 1955)

Female. L 1, L 4, L 7, and L 9 long, L 1 extending beyond tip of D1. Fig. 7,f. Chelicerae with a row of very small teeth on the fixed arm. Leg IV with the usual setae graduated in length from tibia distad. Anal plate with 3 pairs of pre-anal setae and a pair of lunate pores between and slightly behind a line between the posterior pair. Parapodals consisting of one long cigar-shaped plate and a slender one less than half as wide, placed at a slight angle or nearly parallel. Tracheae in contact at the anterior ends, peritreme plate with a bluntly rounded end, Fig. 7,d.

Male not available.

Measurements. Female 0.40 by 0.31 mm. Posterior lateral seta 0.27 mm. Leg IV, 0.50 mm.

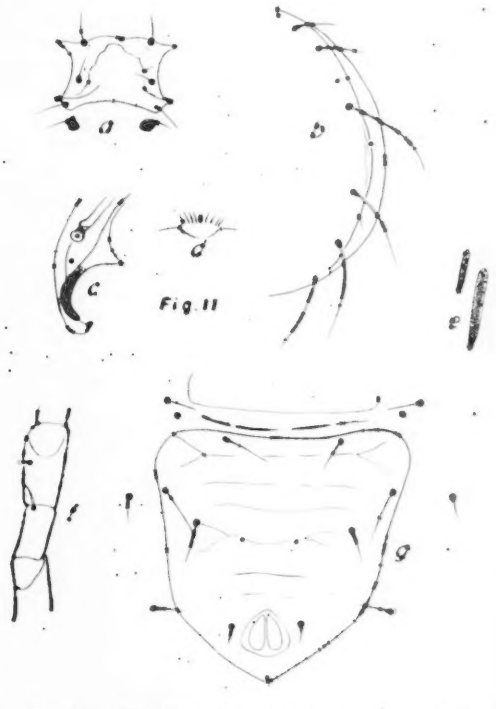

Fig 11

Fig. 11.—*Amblyseiopsis reticulatus* n. sp. a. sternal plate, b. dorso-lateral margin, c. peritreme plate, d. genital armature, e. parapodal plate, f. palpus, g. anal plate.

Habitat. Florida, several locations; feeding on *E. sexmaculata*. Also Bermuda, Mexico, Honduras, Louisiana. Mostly intercepted on shipments of plants into the U. S. A. (National Museum Collection).

Relationships. Characterized by the presence of long lateral setae, the posterior pair equal to body width; also by the presence of lunate pores on the anal plate between the posterior pre-anal setae and almost as far forward. Nearest relative *mexicanus* from which it is distinguished by the circular anal pores (in *mexicanus*) and the parapodals, the accessories being almost as long as the primaries.

Amblyseiopsis largoensis Muma
(Fig. 8) (6, 1955)

Female. Laterals 1, 4, 6, and 8 very long, about half as long as the body width. Leg IV with the usual long setae on genual, tibia and first tarsal segments. D1 and L1 longer than the dorsals and both extending about the same distance forward. Chelicerae with 8 to 9 teeth on the fixed arm. Anal plate with 3 paired setae besides the para anals and a pair of lunate pores close to posterior setae. Setae beside the plate distributed unequally, as in Fig. 8,a. Parapodal plates consisting of an elongate oval one each side, the accessory plates usually present, very slender. Genital armature small as in Fig. 8,a. Peritreme extending forward almost to D1, the plate bluntly truncate at the posterior end, Fig. 8,e.

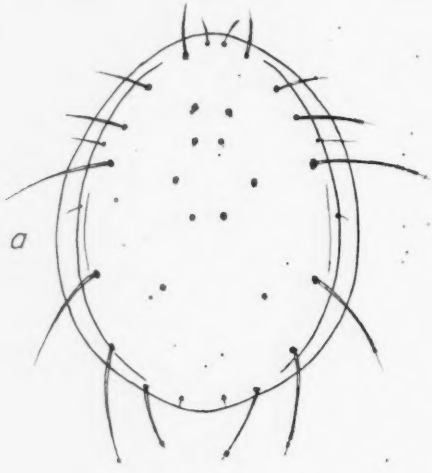

Fig. 12

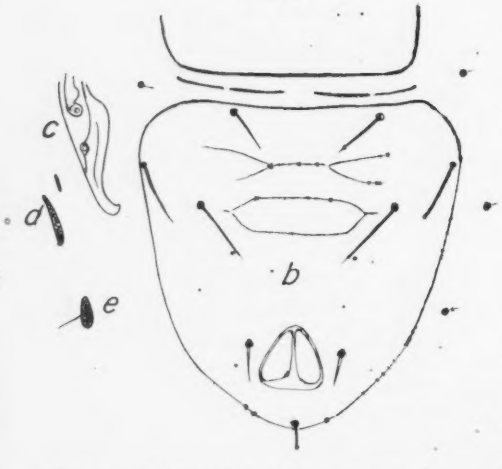

Fig. 12.—*Amblyseiopsis septa* n. sp. a. dorsum, b. anal plate, c. peritreme plate, d. parapodal plates, e. metapodal plate.

Male. Anal plate as in Fig. 8, f with smaller pores than in the female. Of the anterior paired setae of the anal plate, the two posterior ones are almost in line, the pores only a short distance behind.

Measurements. Female 0.36 by 0.24 mm. L9 0.24 mm.

Male.

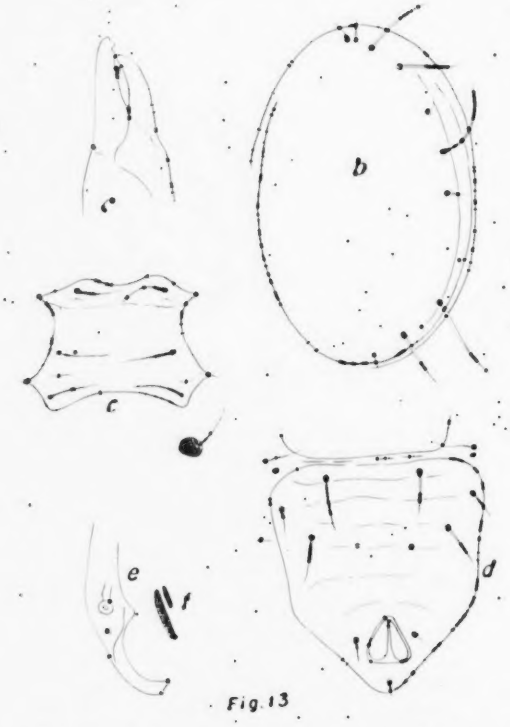

Fig. 13

Fig. 13.—*Amblyseiopsis ovatus* n. sp. a. chelicerae, b. dorsum margin, c. sternal plate and metapodal plates, d. anal plate, e. peritreme plate, f. parapodal plates.

Habitat. On ginger from St. Kitts. L.A. received at Boston Sept. 9, 1933. Muma collected this species from Key Largo, Fla., on lime leaves.

Relationships. The very long L9 and leg IV setae—spacing of the latero-ventral setae (near anal plate), together with character of the genital armature distinguish this species.

Amblyseiopsis potentillae n. sp.
(Fig. 9)

Female. Laterals 1, 4, M2 and L9 long. Chelicerae with about 6 small teeth on the fixed arm. Leg IV with usual graduated setae. Anal plate of the same width as the genital, 3 pairs

pre-anal setae and one pair slit-like or lunate pores slightly behind and mesad of the posterior setae. Pores nearer the setae than to one another. Parapodals parallel, the accessory very slender, about half as long as the primary. Trachaea not quite reaching D1, peritreme plate bluntly rounded at the posterior end, with interior sharp point. Genital armature semicircular with radiating lines from the front margin.

Male. Not available.

Measurements. 0.38 by 0.19 mm. Leg IV 0.38 mm. Long posterior lateral seta 0.14 mm.

Types. U. S. National Museum slides 54-853, 1953, and 54-6277, 1954. Intercepted from Holland at Hoboken, N. J.

Relationships. Characterized by almost parallel parapodals, the position of the anal pores and the length of the posterior lateral setae which are much less than the body width. Nearest species *largoensis* but easily separted by the pre-anal pores and the length of the posterior lateral setae.

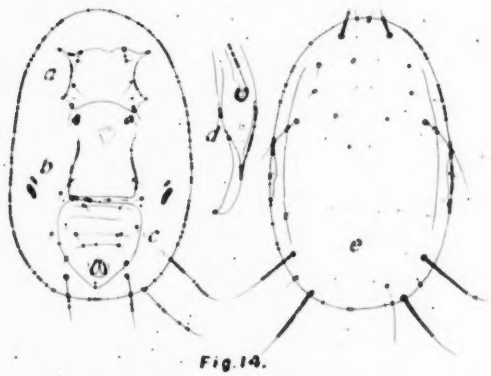

FIG. 14.—*Amblyseiopsis oregonensis* n. sp. a. sternal plate, b. parapodal plates, c. anal plates, d. peritreme plate, e. dorsal surface.

Amblyseiopsis tropicanus n. sp.

(FIG. 10)

Female. Lateral 4, M2 and L9 long. Chelicerae with only 2 or 3 almost indistinguishable teeth on the fixed arm. Leg IV with the usual setae. Anal plate nearly the same width as the genital, with two posterior pre-anal setae each side closer together than the two anterior. Pre-anal pores almost in line laterally with the posterior setae, nearer to one another than to the setae. Parapodals almost parallel, primary much wider at middle, accessories less than half as long. Tracheae extending well between D1. Genital armature semicircular with lines radiating from the front margin.

Male. Not available.

Measurements. 0.35 by 0.22 mm. Leg IV 0.33 mm. Posterior lateral seta 0.09 mm.

Type. Slide SPB Fla. 119141.

Habitat. Bermuda grass, Homestead, Fla. Ipomea, Bossier City, Louisiana.

Relationships. Characterized by only 3 long lateral setae, the presence of circular pores on the anal plate almost if not in line with the posterior pre-anal setae. Nearest species *mexicanus*, but distinguishable by the emarginate anal plate.

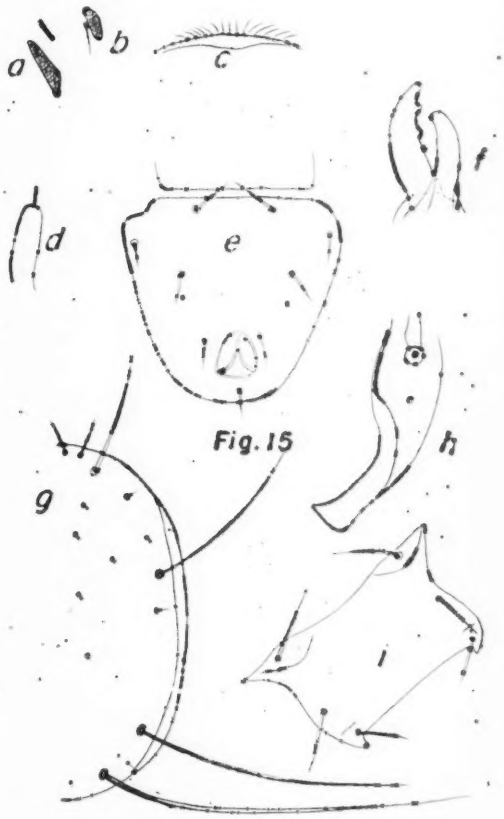

FIG. 15.—*Amblyseiopsis floridanus* Muma. a. parapodal plates, b. metapodal plate, c. genital armature, d. ventral coxal gland, e. anal plate, f. chelicerae, g. dorsal surface, h. peritreme plate, i. sternal plate.

Amblyseiopsis reticulatus n. sp.

(FIG. 11)

Female. Six long laterals including M2. Chelicerae without visible teeth. Leg IV with usual elongate setae, that on the tibia, shortest. Anal plate striate-reticulate slightly wider than the ventral plate. Pores considerably behind posterior setae, but somewhat closer together than to the setae. Parapodals long, slender, parallel, the accessories half as long as the primary. Tracheae not quite reaching D1, peritreme plate obliquely truncate, mesal angle acute. Genital

armature semicircular, anterior margins with radiating lines. Sternal plate striate-reticulate.

Male. Not available.

Measurements. 0.40 by 0.31 mm. Leg IV 0.40 mm. Long posterior lateral seta 0.09 mm.

Type. U. S. N. M. Slides 501, 502, Ex *Neorama plaigula*, Santa Fe, N. Mex. December 1951.

Relationships. Similar to *ovatus*, but with different parapodals and the number of long laterals and the fact that L2 is as long or longer than L1.

Amblyseiopsis septa n. sp.

(Fig. 12)

Female. Laterals 1 to 4 all long, L2 shorter than the others. A total of 7 long lateral setae including M2. Chelicerae with indistinct teeth. Leg IV with usual elongate setae, that on the tibiae shortest. At least 4 long setae on the tarsi. Anal plate striate—reticulate with the usual 3 pairs pre-anal setae, the pores well behind and between the posterior setae, about as close together as to the setae. Parapodals indistinct but primaries long and slender with accessories parallel about as in *sexta*. Tracheae not reaching D1. Genital armature indistinct.

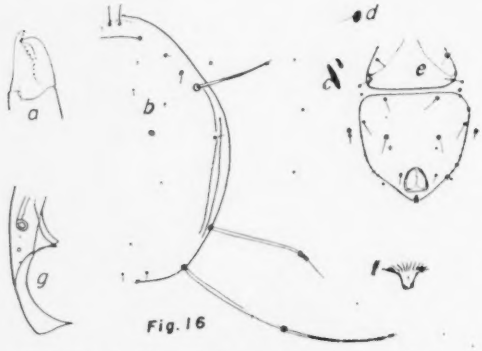

Fig. 16.—*Amblyseiopsis gracilis* n. sp. a. chelicerae, b. dorsal surface, c. parapodal plates, d. metapodal plate, c. anal plate and surrounding setae, f. genital armature.

Male. Not available.

Measurements. 0.40 by 0.31 mm. Leg IV 0.50 mm. Posterior elongate lateral 0.09 mm.

Type. U.S.N.M. Lot 47–14855 on orchid plants Mexico, D. F., at Laredo.

Relationships. Closest to *sexta*, differing mainly in the length of laterals 1–4.

Amblyseiopsis ovatus n. sp.

(Fig. 13)

Female. Laterals L1, L2, L4, M2 and L9 long, others short. Chelicerae with only a few (3–4) teeth and a delicate spine near the tip of the fixed arm. Leg IV with the usual long setae but that on the pre-tarsus longest. Anal plate slightly wider than the genital, striated, circular pores almost as far forward as the posterior pre-anal setae, but nearer together than to the setae. Tracheae just reaching D1, peritreme plates somewhat acute at the posterior mesal ends.

Male. Not available.

Measurements. 0.41 by 0.28 mm. Long posterior lateral seta 0.08 mm.

Type. U.S.N.M. Lot 47–5598 on *Cattleya* sp. from Ecuador at Brownsville, Texas.

Relationships. Close to *americanus* and *oregonensis*, but differs in the dentition of the chelicerae and the position of the pre-anal pores.

Fig. 17.—*Amblyseiopsis elongatus* n. sp. a. sternal plate, b. dorsal surface, c. anal plate, d. parapodal plates.

Amblyseiopsis oregonensis n. sp.

(Fig. 14)

Female. Laterals L 4, M 2 and L 9 fairly short. Chelicerae with 6 to 8 teeth. Leg IV with usual weak setae on genual, tibia and pre-tarsus. Anal plate wider than the genital plate, the pre-anal pores behind and almost in line longitudinally with the posterior pre-anals. Parapodals short but prominent, accessories half the length of the primaries. Tracheae extending forward to D1, the peritreme plate rounded at caudo-mesal end. Genital armature semicircular with radiating lines from anterior border.

Male not available.

Measurements. 0.41 by 0.31 mm. Leg IV 0.48 mm. Long posterior lateral 0.08 mm.

Type. U. S. N. M. Slide No. 7 Lot 52 12630

on Ladino clover, Grants Pass, Oregon, Oct. 22, 1952. Specimens also from sod, apple orchard Yakima Washington; apple leaves Yakima. Also collected in Connecticut.

Relationships. Close to *americanus* from which it differs in the wider anal plate and to *floridanus* from which it differs in the length of M 2 and L 1 as well as the number and size of the chelicerae teeth.

Amblyseiopsis floridanus Muma

(Fig. 15) (6, 1955)

Female. Four long lateral setae, the posterior longest. Chelicerae with three conspicuous teeth on the fixed arm. Anal plate wider than the genital, 3 pairs of pre-anal setae, the pores caudad of the posterior setae, and longitudinally almost in line. Parapodals short, the accessories about half as long. Peritreme plate bluntly truncate at caudo-mesal angle. Genital armature not distinctly semi-circular as in other species.

Male. Similar to the female but smaller.

Measurements. (From Muma's description). Female 0.30–0.34 mm. Mean 0.32 mm. Width 0.21 to 0.22 mm. Male 0.25 by 0.15 mm.

Types. Lake Weir, Florida, Dec. 17, 1952, male allotype, same location Jan. 15, 1952, from litter under trees.

Relationships. Appears to resemble *americanus* closely from which it differs, in the teeth of the chelicerae and the wider anal plate. Examination of types in the U.S.N.M. shows the presence of minute pores on the anal plate omitted in Muma's description and figure.

Amblyseiopsis gracilis n. sp.

(Fig. 16)

Female. Four long laterals including M2. Of these the posterior is very long, about as long as the body width. Chelicerae with 7 to 8 teeth on the fixed arm. Leg IV with the usual elongate setae, that on the genual longest, the ones distad gradually shorter. Anal plate wider than the genital, with the usual pre-anal setae, the pores minute, almost as far laterad as the posterior setae and behind them but much closer to the setae than to one another. Parapodals parallel, short and wide, the accessories also short, less than half as long as the primaries. Tracheae extending forward well between D1, caudo-mesal end of the peritreme plate obliquely truncate.

Male not available.

Measurements. 0.41 by 0.31 mm. Leg IV 0.35 mm. Long posterior lateral 0.31 mm.

Type. U. S. N. M. Lot 46, 5209, from mullein, *Verbascum thapsus*. No. Portland, Oregon, Jan. 29, 1946.

Relationships. Characterized by the very long posterior laterals. Differs from *elongatus* which has the accessories well forward of the primary parapodals.

Amblyseiopsis elongatus n. sp.

(Fig. 17)

Female. Laterals 1, 4, 7, and 9 long. Chelicerae with 7 to 9 small teeth. Leg IV with usual long setae graduated in length distad. Anal plate with 3 pairs pre-anal setae, the posterior closer together than to the anterior. Pores very minute, almost invisible behind the posterior pre-anals and almost as far laterad. Parapodals widely separated, accessory set at a slight angle, and about one-half as long as the primary. Tracheae extending forward to D1.

Male not available.

Measurements. 0.38 by 0.31 mm. Leg IV 0.48 mm. Posterior lateral seta 0.29 mm.

Habitat. Orchid plants from Guatemala at Brownsville, Texas.

Type. U. S. National Museum Lot 51-3021.

Relationships. Nearest relative *gracilis* but distinguishable from this as well as other species by the position of the accessory parapodals which are considerably in front of the primary parapodals.

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ADDITIONAL NOTES ON RHYTIDOPONERA CONVEXA MAYR (HYMENOPTERA, FORMICIDAE)[1]

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A collection of 800 adult specimens of *Rhytidoponera convexa* is the basis of the following notes. These specimens comprise the entire populations of eight separate colonies, so far as it was possible to capture them, and include not only the adults but also all early stages—eggs, larvae, prepupae and pupae. The populations of individual colonies are as follows:

	Number of		
Date of Collection	Adults	Pupae	Larvae
Dec. 22, 1954....	67	24	26
Dec. 22, 1954....	63	23	2
Dec. 22, 1954....	64	11	10
Dec. 23, 1954....	69	56	23
Date not recorded.....	73	1	0
Jan. 10, 1955.....	207	38	0
Feb. 5, 1955.....	82	10	2
	+3♂♂	+2♂♂	
Feb. 14, 1955....	173	0	0

This collection offers an excellent opportunity to check the results recorded from a previous collection (Whelden, 1957) and to extend those results considerably. The previous collection contained no larvae and only one pupa.

The 63 larvae in the present collection include examples of all instars, by far the greater number being the two last instars. The greater number of the larvae occurred singly but there were some which were in five small very compact groups.

In all larvae, small and large, the surface is sparsely covered by rather coarse spines of three distinct kinds. Some are simple, slender objects which are occasionally quite straight but more often are curved or slightly sinuous, and always very gradually tapered to an extremely fine-pointed apex. There is no obvious regularity in the distribution of these simple spines. The second type of spine is more numerous than the first. These are furcate and show great variety. Some are divided almost from the very base into two long, coarse, nearly equal branches. Others are divided only near the apex, where two very slender diverging branchlets are formed. While most commonly the two branches are very nearly equal, not all are so. Unequal branches of all degrees are found, one branch sometimes being scarsely more than a very short acute spine occurring at any point from near the base to one not far from the apex. Infrequently, spines occur in which one or rarely both branches fork a second time, usually into two minute forks at the apex. The third type of spine is much less numerous. In these the apex of the spine bears a radiating whorl of six to eight or even more divergent, often recurved rays. Occasional spines of the second sort have one branch (usually much longer than its mate) ending in a very small whorl of diverging rays. All spines are rather thin-walled, the central lumen extending well out to the ultimate tips. Beneath the base of each spine, there is a single very large cell, accompanied by a second much smaller one, the two being quite unlike the other cells in the hypodermis.

Between the bases of the spines, the cuticular surface of the larva is studded with rows of small conical bosses which form an irregularly reticulate network.

It might well be assumed that the compact groups of larvae noted above resulted from an entangling of these various spines: no doubt these do play a part in holding the groups together. They are not, however, the only, nor even the main cause, for in each of the five groups a tangle of rather coarsely looped fibres was found closely wrapped around and among the spines, but never around the bodies of the larvae. This fibrous tangle held the larvae together in a most tenacious manner. It is to be noted that not one of these groups was formed of larvae of a single size; always there were several sizes, usually in pairs. The most interesting group comprised ten larvae—two very small ones, presumably first or perhaps second instars, and two each of four succeeding instars. One of the larvae of each pair was invariably slightly larger than the other.

The internal anatomy of these larvae is quite like that found in the larvae of other ants, and so calls for little comment. A few details may be noted. The muscles in the posterior part of the body form very broad bands of coarse fibres, associated with which are many conspicuously large oenocytes. The gonads are very obvious from the second instar onwards and show very distinctly that they are formed into three or occasionally four clearly defined units—the three or four ovarioles that will be found in the adult. In the smallest larvae, (presumably first instar), one only was found to be formed of uniformly small cells showing no sign of separation into units. In all other small larvae, the division into parts was apparent, but not as obvious as in

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larger larvae. The gonads comprise two sizes of cells: large cells with large spherical nuclei forming the central region; and around these smaller somewhat elongate cells with small faintly ellipsoid nuclei. These small cells make very clear the occurrence of the three unit parts. The gonads occur on opposite sides of the midgut, near the posterior end thereof. In all but the smallest larvae, favorably oriented sectioning showed very clearly the extremely slender common duct extending downward posteriorly to end near the anus.

Of the several eggs found in one nest, only one is of any interest in this study. In this one a nearly mature embryo is found, in which the gonads are a very conspicuous pair of ellipsoid masses composed of evenly grouped rather large cells each with a spherical nucleus. All the remaining eggs are either newly laid or in very early stages of development.

One would like to use the pupae for a study of organs that occur in adults, for in the latter the thick brittle chitin makes it very difficult to get good preparation in sections. But the organs do not attain their final form and position until very late in pupal development and in some cases not until after the adult has emerged from the cocoon; in either case, not until chitin formation is well advanced. So little attention was given to the anatomy of the pupae.

One fact about these pupae does seem quite interesting, namely the occurrence of two (perhaps three) parasitic organisms. These are definitely rare here, for of the 165 pupae only 4 (perhaps 6) contain a parasite. Each parasitic organism was found in 2 pupae. The first of these is a minute arthropod found in the posterior portion of the gaster among the rather large muscles that occur there. One of the parasites is in a fairly early larval stage, segmentation being very clear, but organ formation showing only a rather coarse digestive tube. This larva lies transversely to the long axis of the host. Development of the second specimen has reached much more advanced stages, its three body parts, head, thorax and abdomen, being clearly formed, but the appendages are as yet only vaguely indicated; apparently there will be three pairs. This specimen is also oriented transversely in the posterior part of the gaster.

The parasites forming the second pair are also arthropods, being quite large acarids. One is apparently fully mature or very nearly so; the other is less mature. This immature specimen occurs in the anterior part of the head, in front of the brain, and above the pharynx and its rather large supporting muscles. Its size is much greater than that of the host brain; indeed, the latter is obviously displaced from its normal position by the enlarging parasite which extends from one side of the head nearly to the other. The posterior wall of the parasite presses closely against the hypodermal layer of the host over a considerable area. The cephalothorax of the parasite is sunk into the muscle, fat-body and gland tissues of the opposite side of the head of the host pupa. The development of the parasite is sufficiently advanced to show clearly the well-developed small cephalothorax, covered entirely by a dense layer of rather coarse hairs which are pressed closely to the surface of the parasite. The abdomen is very large and extremely thin-walled, but very clearly formed of two distinct layers of cells. The outer layer, the body wall, is formed of very thin squamous cells each covering a large area but having only a very small nucleus; the inner layer, which is slightly thicker and formed of smaller cells, is the wall of the stomach which almost completely fills the abdomen. The outer wall of the parasite abdomen is quite smooth, excepting a very small area of the ventral region, anterior to the centrally located anal tube.

The second specimen of this pair of parasites is apparently nearly mature, and measures 3.8 mm. long and 2.6 mm. broad. Its entire surface—cephalothorax, abdomen, legs, mandibles, palpi—all are densely clothed in a thick layer of coarse hairs. The only exception is a narrow zone around the slit-like anal opening occurring in the middle of the ventral surface of the abdomen; this area may be due to the effect of the fixative, causing a slight extrusion of the anal tissues. This parasite was found inside a completely normal *Rhytidoponera* cocoon, in the anterior end. Behind it was the pupa of the host, 6.5 mm. long. This pupa was fully formed so far as external structures were concerned, the body parts, antennae and legs all being well-developed, and chitin formation very distinct. But internally, organ formation was only ghost-like. The entire pupa was but a pitifully feeble dwarf imitation of a normal *Rhytidoponera* adult. Apparently in this case, the parasite had occurred inside the prepupal membrane, but outside the pupal wall.

A third pair of parasites, if such they are, also occurs in mature and apparently quite normal pupae, which they completely fill. There is no indication that there was ever any other organism within the pupae. These two organisms are about equally advanced in development, each being an apparently early pupa. These are distinctly insect pupae, the three body divisions being very clearly defined; but there is no pedicel. The absence of the pedicel definitely rules out the possibility that these are *Rhytidoponera* pupae. Internally, the most conspicuous features are the well-defined flight muscles forming in the thorax, and the gonads in the abdomen. The latter are both ovaries with about thirty well-developed ovarioles in each ovary. Other organs in these two individuals also show slight differences from the corresponding organ in a *Rhytidoponera* pupa

equally developed. Whether these are to be considered true parasites, for the present must remain a question.

This present study of 800 adults confirms all details given in the preceeding note. It does give a slightly wider range of measurements for some parts, but in no case is this more than 2 percent. One correction, perhaps better one emendation, is necessary. It was previously noted that the mandible was full of fat-cells; with of course the usual nerves, trachea and hypodermis. This is not always the case. In this larger collection there are many callows, some very recently emerged (no callows were found in the earlier collection). In the mandibles of these callows, there are many large oenocytes. Presumbably these will gradually disappear, since they are seldom present in obviously older individuals. In this present collection, there are also many individuals which are considered to be very old. In these there is little cellular tissue in the mandibles other than the thin hypodermis and the nerves. Most of the volume is filled with haemolymph.

The callow specimens of this present collection show clearly a feature not found at all in the previous collection, or perhaps occasionally in a very vague form, a feature whose absence caused some concern during the previous study. The two poison glands are about equal in size and extend anteriorly more or less parallel to one another beneath the intestine-rectum wall. One of these glands has a very much wrinkled wall in which very few nuclei occur. In the callows studied here, two very conspicuous branches are found extending from the anterior end of this gland: one of these branches seems usually to extend forward at least to the middle part of the first gastric segment, and to lie close to the chitin wall; the other branch extends forward for a short distance, then turns backwards to end not far from the region of the spermatheca. These two branches are quite tortuous and may occasionally form compact tangled masses about the apex of the thick-walled portion. With increasing age, these branches seem gradually to decrease in size and finally to disappear completely, or nearly so, for occasionally one may note small masses of dark-staining material which appear to be vestiges of them. Certainly, the anterior end of this gland usually shows clearly that no branch is present.

The cells forming these branches are large, irregularly polyhedral objects, each with a moderately large spheroidal nucleus. The branch has no clearly defined central lumen, but often there is an irregular cavity resulting from the failure of the surrounding cells to meet in the central region. The diameter of these branches measures 26–50 μ.

The antennae of *Rhytidoponera* offer but few points of particular interest. Transverse sections of the flagellum show that the several sensory elements occur very symmetrically around the section and quite close together. The only exceptions are the Champagne-cork organs of Forel and the flask-shaped organs of Forel; these two elements are few in number, and occur in a narrow sector in the apical segment and in even smaller numbers in the subapical one. Occasionally one or two may be found in the lower segments. Quite noticeable are the basiconic elements of Berlese (clubs of Forel): these are absent from the first two segments of the flagellum. In segments 3 to 9, they occur in a single ring of seven to nine thin-walled clubs 5–7 μ in diameter, usually not far above the middle of the segment. In the subapical segment, there are often two such rings, at least on the outer half of the segment. The apical segment has four or five such rings, more or less equally spaced from base to near the apex of the segment. All these clubs have rather narrow rounded apices, usually turned rather conspicuously upward. The wall of the club is uniformly 0.4–0.6 μ thick.

Associated with these sensory elements, there are elongate closely massed groups of small spherical nuclei 1.5–2 μ in diameter. Associated with each group, at the outer end, there are several noticeably larger nuclei: some of these are spherical and 3.5–6 μ in diameter; others are ellipsoid or discoid and measure 3–4 x 5–7 μ. Fine nerve fibers pass from these groups out into the bases of sensory elements. These groups of cells form a uniform layer under the entire surface of each segment of the flagellum.

Oenocytes were found in the lower parts of the segments of the antennae of many of these ants. In some specimens, these were conspicuously abundant in the scape and the lowest two or three segments of the flagellum.

Sperms were found in some individuals in every one of the eight colonies considered here. It is to be noted that the presence of even a very small number of sperms is recorded merely as "sperms present". Some details concerning these may be noted. In giving these details, no consideration is given to the number of sperms found in the individuals. This number varied greatly: in some, the spermatheca was completely filled by a dense mass of sperms; in others, the mass of sperms was large but the sperms were in very loose groups; and in occasional individuals, the total number of sperms was very small. Comparison of individuals having large masses of sperms shows many in which the sperms are so oriented as to suggest that a rotary or whirling movement was present; in others, the sperms appeared to be in very irregularly tangled masses. Possibly the first is the state occurring for a short period after the sperms are received; the irregularity is then gradually established.

The percentage of sperm containing individuals varied considerably in the several colonies

the (smallest) lowest being 1.5%, and the highest 15.87%. The four colonies, collected on December 22 and 23, had the following percentages of sperm: 1.5, 15.87, 1.5, and 2.89%. The colony taken on January 10 had 4.34% with sperm, that on February 5, 8.67%, and that on February 14, 3.66%. These figures suggest that there is no particular increase in the number of sperm-containing individuals at any definite season.

Many of the adults contained conspicuously large numbers of mature eggs; even larger numbers contained fewer mature eggs but large numbers of full-sized oocytes, the egg membranes not yet formed. The following colonies are particularly noteworthy in this respect, and show the following correlations: the colony collected on December 22, with 15.87%, containing sperms, had 55.5%, with mature eggs; that collected on the following day (December 23), with 2.89% containing sperms, had 49.3% with mature eggs; the colony collected on January 10, with 4.34%, with sperms, had 23.2% with eggs; and the colony collected on February 14, with 3.66% with sperms, had 14.6%, with eggs. Seemingly there is only slight agreement of sperm presence and egg-laying. It should be noted that an individual containing a large ball of sperms may have few eggs present, or none at all, while another individual with no sperm may contain a very large number of mature eggs. Occasionally an individual may contain so many eggs that much of the gaster seems filled with them (anterior, above, beside and posterior to the stomach, they are present in abundance), and no sperms. Such prolific numbers of eggs are rare however. Usually there are only small numbers present, many contain no eggs whatever. Some of the latter are undoubtedly old.

There remains one added observation to consider—the presence in four colonies of parasitic worms in many of the adults. These worms must profoundly effect the well-being of each colony, and ultimately lead to its destruction. The number of infected individuals varies in the several colonies parasitized: 9.2% in the colony collected January 10; 37.5% in that collected February 5, and 49.4% in that of February 14. The colony whose collection date is not known contained 19.2% parasitised individuals. (In a colony, collected December 22, a single individual was found with worms.)

No very early infection condition was found; but occasionally an individual contained a noticeably small worm with a diameter less than one-third that of most of the worms and very much shorter. There is no indication of the manner in which the parasite enters the ant body. No larva or pupa studied here showed any sign of a worm.

These smallest parasitic worms were found only in the anterior half of the gaster always above or lateral to the stomach. Most of the worms occurred as densely massed coils occupying the greater part of the two anterior gastric segments. The coils were almost invariably very evenly arranged, and in no case formed an irregularly entangled compact mass. Eventually the worm filled almost the entire gaster, the organs of the ant then being greatly compressed and reduced.

Invariably the worm occurred in the body fluid. As above noted the smallest found occurred near the stomach wall, suggesting that at this point may have been the region of entrance. As growth continued, the number of coils of the worm body increased, gradually surrounding the Malpighian tubules and the ovarioles, which for some time seemed to be uneffected by the parasite. Effect must, however, appear in time. The first structure to show any effect seemed always to be the fat-bodies and oenocytes and then the ovarioles, especially if the latter contained large oocytes, for the oocytes showed very clearly a thinning of cytoplasmic contents. Eventually all organs became exhausted, the stomach and the muscles in the posterior end being the last to show these changes. It would appear that the mature worm escapes simply by growing enough to press the large anterior gastric segment off like a lid.

The mature worm may occupy only the gaster, such is the case in a very large majority of the infected ants. Infrequently, the worm is contained in the thorax only. Individuals were found with the parasite partly in the thorax and partly in the gaster, the greater part of its body being in the gaster. Occasionally, an ant was found with the parasite extending from the head through the thorax and into the gaster. In rare cases the worm seemed to be entirely in the head at the time the ant was collected. The head cavity seems scarcely large enough to contain a mature worm. So it would seem that to reach maturity, a worm so found must eventually reach into other parts of the body.

What individuals are infected? This present study indicates that any adult can become parasitized; certainly, at least as many individuals with sperms in the spermatheca were infected as not. The capacity for immediate egg laying also shows no relation to parasite presence; an ant with numerous mature eggs may contain one or even two apparently mature worms. But eventually both sperms and eggs must disappear as the parasite enlarges. No callows nor males were found containing a worm. Eventually it would seem that all individuals of the colony must become parasitized; then the colony would die.

SUMMARY

A total of 800 adults, 165 pupae and 63 larvae of *Rhytidoponera convexa* Mayr were prepared suitably and studied in detail, the results supporting facts previously given, and extending them considerably.

The 63 larvae included examples of all instars;

some occurred singly and some in small compact groups. All larvae were armed with spines of three kinds: some simple, some once or twice furcate, and some with radiating branchlets at the apex. It was partly due to these spines that the groups were maintained: but a more important cause was the presence of an entangling skein of coarse fibre.

The pupae were found to contain two kinds of parasites—one a small arthropod found in the posterior part of the gaster, the second a large hairy mite occurring in the head or in the head region. There were also two pupae, in cocoons apparently exactly like the others, but they are insects and are definitely not *Rhytidoponera*, lacking any pedicel.

The callow adults show the presence of two rather conspicuous branches extending from the apex of one of the poison glands. These branches seem to be lost as the ant gets older, only a few being found in the older adults.

The anatomy of the antennae is discussed briefly.

Sperms and also mature or nearly mature eggs occur in many adults. There is no correlation between the presence of sperms and that of mature eggs, nor does the number of sperm-containing adults reach a maximum at any time.

Parasitic worms are found in many of the adults in several of the colonies.

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ON THE ORIGIN OF THE EXTERNAL GENITALIA OF INSECTS[1]

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INTRODUCTION

In a recent morphological study of the abdomen of a machilid and a rhaphidiid the writer (1957) found strong indications that the external insect genitalia are sternal in origin, as was maintained by Heymons (1896a–1899b). This is contrary to the currently accepted theory that the genitalia are modified limbs. The present essay is an attempt to investigate these indications further through search of as much pertinent literature as possible, so as to determine how well Heymons' original idea is supported. It also attempts to discover how and why, if the genitalia are of sternal origin, this theory has been neglected in recent years; or, if the limb theory of the origin of the insect genitalia can be justified, how secure are the grounds on which it rests. The present survey, therefore, is secondarily a search for the sources of confusion and discrepancies, and for the problems involved therein.

Before entering into discussion it seems advisable to clarify the usage of some morphological terms employed in this paper. The term gonapophysis is used in a wider sense than it is defined in Snodgrass' textbook (1935a). One reason for this is the need for repeated references to the older authors who used the word in this broader sense. As used here, the term gonapophysis is not necessarily restricted to the endite of the gonopod, but is applied to any ventral reproductive tubercle or extension of the body surface forming the ovipositor of the female or the phallic organs, including the paramere and phallus, in the male. Terms employed by various authors are used here as they appeared in their papers. Some of these are accompanied by more commonly used equivalents in parentheses, while others are explained elsewhere. The more important of these are the following: *anterior valves* or *valvulae* represent the gonapophyses of the eighth segment in the female and are the first valvulae of Snodgrass; the *lateral valves* or *valvulae* are the gonapophyses of the ninth segment and are the third valvulae of Snodgrass; and the *inner valves* or *valvulae* and *posterior valves* or *valvulae* are also the gonapophyses of the ninth segment (usually homologized with the anterior valvulae of the eighth segment) and are the second valvulae of Snodgrass.

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EMBRYONIC ABDOMINAL APPENDAGE RUDIMENTS

Since the embryonic abdominal appendage rudiments of the eighth, ninth, and tenth segments are thought to give rise to the external genitalia of insects according to the currently

accepted theory, it seems appropriate to review our knowledge of them.

The existence of embryonic abdominal appendages homodynamous with the legs has been recorded in most major groups of insects, but opinion has been divided both as to their appendicular nature and as to whether they persist in postembryonic life—and if so, in what form. The issue has centered especially upon the destiny of those occurring on the eighth, ninth, and tenth segments. Two workers have reported that these appendage rudiments give rise to the ovipositor in the female and to the phallic organs (paramere and penis) in the male.

Wheeler (1893), in his embryological study on *Xiphidium* (Tettigoniidae, Orthoptera), claimed that the appendage rudiments of the eighth and ninth segments give rise directly to the anterior and posterior valves (first and second valvulae) in the female, while the third valvulae probably arise from the tenth segment; in the male the appendage rudiments of the tenth segment disappear late in embryonic life, but probably give rise to the genitalia. Else (1934) found that in *Melanoplus* (Locustidae, Orthoptera) the appendage rudiments of the tenth abdominal segment, after forward migration above the ninth segment, give rise directly to the male phallic organs.

All embryological studies on orthopterous insects show that appendage rudiments appear on almost all the abdominal segments. This is true in *Blatta* (Cholodkowsky 1888–1890, Patten 1884), in *Mantis* (Graber 1888, 1890), in *Oecanthus* (Ayers 1884). Roonwal (1937), in his embryological study on *Locusta*, said that the appendage rudiments of the eighth segment are reduced in later embryonic life and probably disappear, and the appendage rudiments of the ninth segment give rise to the lateral valves (third valvulae) of the ovipositor in the female; in the male the rudiments on the tenth segment later fuse with those of the ninth segment, and these together produce the male genitalia. The appendage rudiments anterior to the eighth segment disappear earlier, except for those of the first segment which are called the pleuropodia. Graber (1890, fig. 86) showed that in *Stenobothrus* the eighth to tenth abdominal appendage rudiments appear after those of the preceding segments have disappeared, but he did not study the postembryonic development of these rudiments. The appendage rudiments on the genital segments in *Blatta*, *Mantis*, and *Oecanthus* disappear late in embryonic life. The development of genitalia from appendage rudiments seems to have been observed only in these embryological studies on the species of Locustidae (Acrididae) and Tettigoniidae.

In Heteroptera Heymons (1896b, 1899a) showed that no appendage rudiments occur in *Nepa*, *Notonecta*, *Naucoris*, *Cimex*, and *Pyrrhocoris*, except for those of the first abdominal segment.

Among holometabolous insects the occurrence of abdominal appendage rudiments in the embryo has been recorded in Hymenoptera, Lepidoptera, Trichoptera, Coleoptera, and Neuroptera. In Hymenoptera Butschli (1870) and Graber (1890) observed them on all abdominal segments in *Apis* and *Hylotoma* respectively, but Carriere and Bürger (1897) found them only on the third and fourth segments in *Chalicodoma*. In *Apis* they were seen only in very early stages of embryonic development. In *Hylotoma* they appear on all segments, but disappear very early except on those segments where the larval legs occur.

In Coleoptera Graber (1890) showed that there are appendage rudiments in *Melolontha* on the second to the tenth segments and that they enter into the formation of the lateroventral walls of the abdominal segments; in *Hydrophilus* he found them on the first to the ninth abdominal segments.

Graber (1890) wrote that in *Lina* (Lepidoptera) the appendage rudiments are seen on rare occasions, and when they do appear they can be recognized for only a brief period. In *Sphinx*, according to Kowalevsky (1871), abdominal appendage rudiments occur on eleven segments in the very early stages of development. In *Bombyx* (Tichomiroff, 1882; *cf.* Graber, 1890) weak segmental structures hardly warranting the the name appendages occur on the second to the tenth segments, and they completely disappear later except for those on the ninth and tenth segments.

So weak and ephemeral are the embryonic abdominal appendage rudiments in Lepidoptera that Graber (1890, p. 703) found it impossible, first, to state definitely whether these anlagen have a slight, continuous development or not, and, second, even granting their appendicular nature, to determine at the then current state of knowledge of the abdominal appendages whether these are primary or secondary. Korschelt and Heider (1892) suggested that although the embryonic abdominal appendages disappear they are not completely lost, their vestiges remaining latent for a time, and are reactivated later, in the larva, to form the larval legs. Friedmann (1934) shed more light on this point. She showed that appendage rudiments of morphologically equal value appear on all segments in *Chaerocampa* and *Odonestis* in a very early stage of embryonic development, and that those of the third, fourth, fifth, sixth, and tenth segments become the larval legs through a continuous developmental process. Since the abdominal legs of the larva undergo the same developmental processes as the thoracic legs, they should be regarded as true appendages. The appendage rudiments of the other segments are vestigial from the beginning, and disappear during the later part of embryonic development. Eastham (1930) obtained similar results in

Pieris. Thus the appendicular nature of the abdominal legs seems to be established; but, as indicated above, the leg anlagen disappear in *Lina*, *Sphinx*, and *Bombyx* before the development of the prolegs. The hypothesis of Korschelt and Heider seems to offer the best explanation of this.

In Neuroptera, Trichoptera, Hymenoptera, and Coleoptera, where more conspicuous larval legs occur on more segments, there seems to be no doubt that they are true appendages homologous with the thoracic legs. They have been so regarded in recent works, from Snodgrass (1931) to Pryor (1951). Hinton (1955), however, believes that the larval prolegs are secondary developments. In spite of his evidence supporting this contention, the embryological works of the nineteenth century so abundantly uphold the appendicular origin of prolegs that Hinton's heterodox view is dismissed for the present. The hypothesis of Korschelt and Heider is at least an important alternative explanation of the origin of larval prolegs. Hinton apparently failed to refer to this hypothesis.

Patten (1884) showed rudimentary appendages on the anterior three abdominal segments of *Neophalax* (Trichoptera). Heymons (1896d) found that the filamentous abdominal gills of *Sialis* (Neuroptera) develop from ventral abdominal epidermal thickenings which arise from appendage rudiments, and that the tracheal gills of *Ephemera* (Ephemeroptera) have a similar origin. Heymons (1897a) also showed that the styli of *Lepisma* (Thysanura) arise from appendage rudiments.

It is clear from the foregoing review that there are no appendicular anlagen in the embryo which might later give rise to the external genitalia, at least in Thysanura, Ephemeroptera, Heteroptera, Neuroptera, Hymenoptera, Trichoptera, Lepidoptera, Coleoptera, and Orthoptera (except Locustidae and Tettigoniidae). It might be suspected that the embryonic rudiments, after the lapse of a latent stage, reappear on the eighth and ninth segments as gonapophyses. That this supposition is highly improbable will be shown later in discussing the origin of the female genitalia.

THE CONCEPT OF THE ABDOMINAL STERNUM

The presence of the embryonic primary sternum has long been recognized, and the appendage rudiments have always been observed on either side of it. Heymons (1899b) claimed that the abdominal sternum is composed of three parts, the median field and two lateral fields, this being the primary condition. He found the median field to be associated with the formation of the segmental ganglia, while the lateral fields tend to be pressed in by the flattened appendage rudiments. Haase (1889), who first elucidated the presence of the primary sternum, thought its three-part subdivision (Dreitheiligkeit) to be superficial, and regarded the lateral fields as merely the flattened appendage rudiments. Börner (1904), on the basis of comparative anatomy, also found the three subdivisions of the sternum in Chilopoda homologous with the median field of the sternum in Hexapoda, and agreed with Haase that the lateral fields of the hexapod sternum correspond to the appendage fields of the thorax and of the abdomen in Chilopoda.

Ford (1923) also observed the division of the sternum into a median field and two lateral fields in Mantaria, Phasmaria, Tridactylidae, Acrydiidae (=Tettigidae), Tettigoniidae, and Gryllidae, but not in Blattaria, Acrididae (=Locustidae), Dermaptera, Plecoptera, Odonata, and Ephemeroptera. She thought it doubtful that the divisions are primary. Roonwal (1937) found the three divisions of the sternum in the embryo of *Locusta*, from the mandibular segment to the tenth abdominal segment, and said briefly that the lateral fields bear appendages. The writer (1956) was inclined to believe that the lateral fields of the sternum are primary. In the pleurosternal region of the adult thorax in such a primitive insect as *Blatella* the well defined subcoxa adjoins externally the well defined sternum, and between these two the sternal apophysis (furca) arises internally. Therefore the sternal apophyses may represent the lateral fields of the primary sternum.

What must be emphasized is the presence in the abdomen of the primary sternum, which occupies considerable space on the midventral portion of the abdominal segments. Recent workers have tended to neglect the presence of this primary sternum, due (as will be shown later) to the preconception that the modified abdominal limbs are supposed to be approximated to each other along the midventral longitudinal axis.

HEYMONS' THEORY VERSUS THE THEORY OF LIMB ORIGIN OF THE EXTERNAL GENITALIA

Prior to Heymons, Lacaze-Duthiers (1849–1853) regarded the gonapophyses of insects as modified sclerites of their respective urites (segments). Grassi (1888), Haase (1889), and Peytoureau (1895) also concluded that each gonapophysis is a secondary ectodermal development. Heymons (1896–1899) was the foremost proponent of the concept that the gonapophyses are hypodermal (ectodermal) processes confined to the Insecta. Primarily as a result of his embryological studies, he maintained that (1) The gonapophyses of the eighth segment (first valvulae) and the inner gonapophyses (second valvulae) of the ninth segment in the female arise from the median field of the primary sternum; (2) The lateral gonapophyses (third valvulae) of the female are a secondary development phylogenetically and are displaced posteriorly by the styli during the course of nymphal development; (3) In Orthoptera the abdominal appendage rudi-

ments of the ninth segment give rise to the styli, which degenerate in the female during the course of development; also, the abdominal appendage rudiments produce the segmental styli in *Lepisma* (Thysanura), the styli and cerci being the remnants of the abdominal legs; and the tracheal gills in Ephemeroptera and the filamentous gills in *Sialis* (Neuroptera) are secondary developments (gliedmassenähnliche Abdominalanhänge) that arise after reduction of the remnants of true appendages such as styli; (4) The gonapophyses usually arise after the appendage rudiments have disappeared—more precisely, after they have gone to form the lateral ventral plates of the abdominal segments. Thus, according to Heymons, the gonapophyses and the abdominal limbs differ in origin, both in time and in place of occurrence.

First opposed by Weismann (1866), Lacaze-Duthiers' view yielded place to the theory that the gonapophyses represent modified ventral abdominal appendages homologous with the thoracic legs (Ganin, 1869; Packard, 1871; Kraepelin, 1873; Dewitz, 1875; Cholodkowsky, 1891; Wheeler, 1893). Ganin, Kraepelin, and Dewitz referred to the ovipositor anlagen under the general term "Segmentanhängen," and described them as "Epidermisverdickungen," "Zapfen," or "Imaginalscheiben," homologizing them with the thoracic legs but giving no good reasons for so doing. Zander (1899, p. 326), commenting on their uncritical acceptance of the appendicular nature of the gonapophyses, remarked that it had not been established even then that these sexual appendages (Geschlechtsanhänge) develop from the appendage anlagen occurring in the embryo.

Dewitz (1875), studying the embryo of *Locusta* (Locustidae, Orthoptera) just before hatching, observed the gonapophyses arising from the imaginal discs found on the appendage rudiments, and said that the gonapophyses are therefore of limb origin. Wheeler (1893), working with embryos of *Xiphidium* (Tettigoniidae, Orthoptera), tried to supplement Dewitz' observation. He said (p. 135): "Up to the time of hatching the gonapophyses could be continuously traced from the appendage rudiments." Although admitting on the same page that "the mere fact that these appendages arise from imaginal discs (Dewitz) is not sufficient evidence of their homodynamy with ambulatory appendages," he does not state whether imaginal discs are formed in *Xiphidium* or not. Thus Wheeler apparently did not completely support Dewitz' observation. Peytoureau (1895) and Heymons (1896c) tried to explain this discrepancy by suggesting that possibly the rudiments of the gonapophyses appear precociously in the embryos of Locustidae before the abdominal appendage rudiments disappear, in contrast to their later appearance, after the appendage rudiments have disappeared, in Gryllidae. This precocious appearance of the gonapophyses, according to Heymons and Peytoureau, obscures the actual picture. As already noted, Graber's figure (1890, fig. 86) of the embryo of *Stenobothrus* (Locustidae) clearly indicates that the appendage rudiments of the eighth, ninth, and tenth abdominal segments appear after those of the preceding segments have disappeared. Whether these appendage rudiments represent the true appendages (as Graber unconditionally believed) or whether they are the anlagen of the sternal gonapophyses is open to question. Since all the abdominal appendage rudiments appear in all other insects at about the same time, in very early stages of embryonic development, the writer suspects that they are probably the anlagen of the gonapophyses which are sternal in origin.

Heymons' theory met with severe opposition from Verhoeff, which resulted in extensive polemics between them (1896-1899). The main issue was whether the cerci, styli, and gonapophyses are true appendages or not. Heymons regarded the styli as remnants of the limbs, but denied this origin for the gonapophyses.

For Verhoeff the gonapophyses were also the limbs. This disagreement stemmed from differences in their concepts of true appendages. Heymons saw the true appendages as the structures arising from the primary limb rudiments (Gliedmassenanlagen), and regarded them as homodynamous with the thoracic legs. Verhoeff (1896) gave a different definition: real segmental appendages are structures with at least two segments that can be moved by at least one muscle, segmental appendages which lack these characteristics being either reduced true appendages or ones which have never had these attributes and are evolving toward true limbs. Verhoeff, considering only the comparative anatomy of adult arthropods, thus defined the appendage in a narrower sense. He claimed to have found that the first segment of the gonapophyses in *Machilis* is muscled, and also that the parameres of some Coleoptera, Hymenoptera, and Diptera are two-segmented (1897, 1902). These observations were refuted by Heymons (1897b) and Börner (1904). Taxonomists as well as morphologists today do not admit the correctness of Verhoeff's observations. If parameres in these higher groups of insects look segmented, the segmentation is not primary but can more properly be interpreted in secondary, mechanical terms.

Heymons and Verhoeff never understood each other, due apparently to their totally different approaches to the problem. Although, as Verhoeff claimed, the current concept of homology was based primarily upon adult structures, when embryological evidence becomes available it should be given at least equal weight. The more circumstantial evidence becomes available, the sounder the interpretation that can be made.

The "ein Ei ein Vogel" principle, in which Verhoeff completely lacked confidence, holds true for many structures, especially when we are concerned with morphogenesis in which only the ectodermal cells are involved. The rudiments of the thoracic legs always give rise to the thoracic legs. Objections may be made to this approach in the light of certain dazzling results of experimental morphological studies, such as homoeosis, which indicate diverse potentialities of ectodermal cells in morphogenesis. But we are concerned with probable morphogenesis under natural conditions, not with the potentialities or possibilities which are the concern of experimental morphologists. Homoeosis may possibly be a mechanism of macroevolution but, while insects are still insects, the "ein Ei ein Vogel" method is still a good, reliable one to be retained for the study of homology. The reliability of this method will be further increased with improved comparative knowledge of the tissues involved in the morphogenesis of certain structures.

Verhoeff (1902, p. 73) summarized his concept in the following scheme:

A. Lepismidae and Machilidae

♀ 8th abdominal segment:	2 gonocoxites, 2 telopodites
♀ 9th abdominal segment:	2 gonocoxites, 2 telopodites
♂ 8th abdominal segment:	2 gonocoxites (*Machilis*) or coxosternum (*Lepisma*), 2 telopodites
♂ 9th abdominal segment:	2 gonocoxites, 2 telopodites

B. Pterygota

♀ 8th abdominal segment:	2 gonocoxites or coxosternum, with or without 2 telopodites (anterior ovipositor valvulae)
♀ 9th abdominal segment:	with or without 2 gonocoxites, never with coxosternum; with or without 2 telopodites (posterior ovipositor valvulae)
♂ 8th abdominal segment:	coxosternum, 2 telopodites or syntelopodite, or only 1 telopodite
♂ 9th abdominal segment:	coxosternum (always?), 2 telopodites, parameres or syntelopodite (present or lacking).

Verhoeff's theory was accepted with but slight modification by later workers, notably by Börner (1904, 1921), and by Crampton (1917–1938) in his series of papers. As to Crampton's work, it will suffice here to say that he actively engaged in searching for the supposed ancestral biramous limbs in insect genitalia. The theory of limb origin of insect genitalia thus became established almost to the point where a great majority of later workers, consciously or unconsciously, tried to make their observations fit this theory. Heberday (1931) and Friedmann (1934) are the only workers, as far as the writer is aware, who still defended Heymons' theory.

It will be clearly seen from the foregoing historical review that the theory of limb origin of genitalia had not been well founded in works earlier than that of Wheeler (1893). At that time the only evidence that the abdominal appendage rudiments give rise directly to the genitalia was supplied by his work; but Wheeler's observations, though perfect on their face, are not free from suspicion as to their precision, as has been indicated by Peytoureau, by Heymons, and by the writer in this work. It must also be remembered that Verhoeff's theory was based on the comparative anatomy of adult Arthropoda, with complete neglect of the embryological evidence then available, while Heymons' theory of the sternal origin of the genitalia was based on many facts observed by Heymons himself (1891–1896). Considering the circumstances, it seems worth while to examine the works subsequent to Heymons and Verhoeff, to see which of the two theories better explains the origin of the external genitalia of insects.

ORIGIN OF THE FEMALE EXTERNAL GENITALIA

The description and figures by Christophers and Cragg (1922) of the development of the ovipositor in *Cimex* seems to support Heymons' theory very convincingly, though these authors apparently were not aware of the problem involved. According to them (p. 456), "The nymphal eighth segment produces the anterior gonapophysis and the nymphal ninth sternum differentiates into a central depressed portion and lateral raised areas which become the lateral sternal areas. Arising from this depressed portion, on either side of the middle line are clearly seen two flattened projections, the rudiments of the gonapophyses of the ninth segment . . (17 lines) . . . the bases of the chitinous strip on the gonapophyses. These processes, which we have seen are at first situated near the middle line, are carried by the widening of the oviductual margins far to the side; it is this which causes them to appear in the adult as appendages from the lateral portion of the ninth sternite. We have already seen that they originate as projections from the median depressed area."

This description, as well as the figures, clearly show the three divisions of the sternum in the nymph, and also show that the gonapophyses arise from the median field of the sternum, as Heymons maintained. It is noteworthy too that the narrow strip at the base of the gonapophysis, which is the ramus in taxonomy and apparently is the homologue of the valvifers in other orders of insects, arises from the primary sternum.

The sternal origin of the valvifers has been asserted several times in the past. In Hymenop-

tera, Zander (1916) has shown for *Apis*, and D'Rozario (1942) for *Apis* and *Vespula*, that the valvifers represent remnants of the eight and ninth sterna—which was the conclusion reached by Christophers and Cragg in their study on *Cimex*. However, D'Rozario said (p. 383) there is a possibility that the valvifers represent coxosternites instead of coxites alone. This interpretation is unfounded, since apparently he was trying to conform to Snodgrass (1935) as cited by him on the same page. Snodgrass himself (1935b) observed that the first valvifer in Gryllidae arises from the sternum, and admitted (p. 51) that he had to make this fact fit with the theory of limb origin of the gonapophyses. At any rate, the embryonic appendage rudiments in Hymenoptera, and especially in *Apis*, are very weak developments that occur only in the early part of embryonic development. We can not derive the gonapophyses from them.

That the valvifers are the sternum in Orthoptera has been asserted by Walker (1919, 1944) on the basis of postembryonic development, and by Ford (1923) on the basis of musculature. Snodgrass (1935b), as mentioned above, also observed that the first valvifer arises from the eighth sternum.

In Neuroptera, Matsuda (1957) has suggested that the valvifer of the ninth segment should be sternal in origin, basing his conclusion on the musculature associated with it and the musculature associated with the clearly defined eighth sternum, which bears the first valvulae in *Agulla*. He has also indicated in the same paper that if we discard the limb concept of the origin of the gonapophyses and replaced it by Heymons' theory, direct homologies both in external structures and in musculature are possible between the female genitalia of Thysanura and those of lower groups of neuropteroid insects such as *Agulla*, *Bittacus*, and *Tipula*. In these lower neuropteroid forms the first valvulae are connected and musceled directly by the eighth sternum, as in Machilidae; and Matsuda thinks that the valvifer is a secondary development in phylogeny which has attained its highest degree of complexity in Orthoptera, Hymenoptera, etc.

The studies cited above show clearly that the valvifers are sternal in origin. It should be pointed out that they have been interpreted as parts of the coxites purely on theoretical grounds. If the valvifers which bear gonapophyses are sternal in origin, there is no reason whatever to regard the gonapophysis as the endite of the coxite. It might be suspected that the embryonic appendage rudiments had reappeared, after lapse of a latent stage and migration to the sternal region, as the gonapophyses on the midventral parts of the eighth and ninth segments. This, though, is a highly complicated hypothesis and virtually impossible to demonstrate, since it involves two assumptions, namely, the reactivation of the rudiments of the gonopophyses and their migration to the sternum. Moreover, the styli occur on the same segment with the gonapophyses in Thysanura. When two structures of different embryological origin occur on the same segment, the one structure can not be derived from the other. It is most improbable that the embryonic appendage rudiments should disappear, then reappear later as the gonapophyses.

It was noted above that their different times of appearance was one of the criteria used by Heymons in distinguishing the gonapophyses and the structures arising from the embryonic appendage rudiments. It is interesting to see how well this criterion holds up in the works published after Heymons.

Zander (1899), working on the postembryonic development of the ovipositor of Hymenoptera, supported Heymons' theory on the basis of the embryological evidence then available. He said (p. 329): "All these facts show us plainly that the first anlagen of the embryonic abdominal appendages and of the gonapophyses belong to two distinct epochs of development in Hymenoptera also. The former are of purely embryonic nature and are demonstrable only during embryonic life, the latter are first established in the larval stage." Walker (1919) generalized the mode of development of the female ovipositor in Orthoptera, and said (p. 277): "Where styli occur, they may appear at an earlier stage than the papillae which are destined to form the valvulae . . ." This statement means that the styli, which are remnants of the limbs, appear earlier than the gonapophyses. Qadri (1940, p. 145), referring to blattids, said: "It may be pointed out that in the early part of the nymphal life the coxites of the eighth and ninth segments alone are differentiated, while the anterior and posterior valves [first and second valvulae] arise from them some time later during the following nymphal growth. Denny, in *Blatta*, also refers to the absence of the anterior and posterior valves during the first and second stadia." This statement clearly indicates that the ovipositor and the coxites differentiate at different times. Many more examples can be cited from recent works, but these examples will be enough to show the general soundness of Heymons' criterion. In the Acrididae (Locustidae), Qadri said (1940, p. 156) that the female genitalia are recognizable in the pronymphal and the first instars. He said also (p. 148) of the Tettigoniidae: "In the youngest nymph collected, measuring about 5 mm. in length, the ninth sternum is bilobed posteriorly. These posterior lobes are much thicker and appear to represent the appendages of the ninth segment." These statements are in accord with observations by Dewitz (1875) and by Wheeler (1893) on species of Locustidae and Tettigoniidae. In these families the gonapophyses seem to appear much earlier than in other groups of Orthoptera.

Heymons also believed that the posterior val-

vulae (second valvulae) arise from the ninth primary sternum. When styli occur in Orthoptera they persist only in the male, disappearing in the female during nymphal development. The lateral valvulae (third valvulae) are displaced posteriorly during the course of nymphal life. Roonwal (1937) stated simply that the ninth pair of abdominal appendages persists in the female of *Locusta* as the upper (third) valvulae. Michener (1944) thought that the third valvulae are homologous with the styli. Thus there is great diversity of opinion regarding the origin of the third valvulae.

Roonwal's description is extremely short. Moreover, he worked on a species of Locustidae, and in this group the development of genitalia is confusing. Therefore his work is not considered at length here. The second valvulae always appear later than the third valvulae, and seem to arise as a bifurcation or outgrowth of the latter (D'Rozario, 1942; George, 1928; Nel, 1929). George's description and illustrations seem to show this especially convincingly, although he interpreted the second and third valvulae as coxites on theoretical grounds. If the second and third valvulae have the same origin (though Heymons did not so indicate clearly), they should be either sternal or coxal. Their sternal origin is strongly indicated, as has earlier been shown in this paper. The musculature associated with the third valvulae, and that of the stylus also, seems to indicate that the third valvulae are sternal in origin. When present, the stylus is always muscled from the coxite, and this constant musculature is recognized as a good morphological landmark to identify the stylus. The third valvulae are never muscled from the coxite, but usually from the ninth tergum only, though Snodgrass (1935b) said that in *Dissosteira* they are also muscled from the basal apodeme of the ovipositor, which is probably sternal in origin. Since the musculature clearly indicates that the stylus and the third valvulae are of different origin, the only probable origin of the latter is the sternum. The external structure associated with the third valvulae also suggests that they are the sternum. The second and third valvulae are usually connected with the valvifer which is sternal, and therefore they are likely to have the same origin and to be sternal structures.

ORIGIN OF THE MALE GENITALIA

On the question whether the male external genitalia of insects are of appendicular origin or not, workers have been somewhat less definite than for the female genitalia. Wheeler (1893) found that the tenth abdominal appendage rudiments of *Xiphidium* move up to the posterior margin of the ninth pair (p. 121) and disappear (p. 118), but he thought that probably the appendage rudiments of the tenth segment have migrated to the ninth segment to form the male genitalia.

Zander (1900, 1901, 1903) is the founder of the modern concept of the morphogenesis of the male genitalia. He worked on their postembryonic development in Hymenoptera, Trichoptera, and Lepidoptera, and summarized his results (1903, p. 589) as follows: In the three insect groups studied the genital appendages arise from anlagen of precisely the same value. The homologies are seen "(1) In the anlage of a postembryonic invagination (genital pocket), variable in form, of the twelfth [ninth abdominal] segment; (2) In the development of a pair of simple, primitive tubercles at the bottom of the genital pocket; (3) In the secondary division of each tubercle into a lateral (valva) and a median one; (4) In the formation of the penis from originally paired anlagen." The most significant point here is his discovery of the division of each genital lobe, the resulting median parts of these then fusing to form the penis, while the lateral parts become the parameres situated on either side of it. In Hymenoptera, each of these lateral lobes divides further into two lobes. They are the inner and outer claspers (D'Rozario, 1942) or the penis valve and clasper, respectively, in taxonomy. These two structures together should correspond to the parameres of other orders of insects, as D'Rozario (1942) contended. It should be noted also that Zander found that the male genitalia always arise from imaginal discs in the forms he studied.

Meanwhile, Heymons (1896c, p. 202) had remarked, in the absence of evidence for the limb origin of the male genitalia, that the sexual appendages of the male are no more to be derived from segmental masses than those of the female, and said that an entirely different derivation for these two sorts of structures must be thought unlikely. After Heymons and Zander the majority of workers began to adopt the limb theory of the origin of the male genitalia, though no concrete evidence existed in its support.

Verhoeff (1896–1902), Walker (1922), Singh-Pruthi (1924), George (1928), Metcalfe (1932), Michener (1944), and others, have regarded the male genitalia as derivatives of the ninth pair of abdominal limbs and homologous with the posterior (second) valvulae of the ovipositor. Gustafson (1950) tried to derive them from the ninth segment, and homologized the gonapophyses with the eversible sacs in pregenital segments in Thysanura. This is essentially the same view as that of Silvestri (1902), who contended that the gonapophysis is an eversible sac permanently everted. Gustafson, however, apparently was mistaken on one very critical point. He said (p. 50): "The ampullae in the tenth abdominal appendage rudiments form the gonapophyses of both male and female and phallus of the male," but gave no grounds for this positive statement.

Embryological evidence shows that the ampullae of the tenth segment later unite as an anterior part of the median ejaculatory duct (Heymons, 1897a; Snodgrass, 1937), or that they are the rudiments of the accessory glands (Else, 1934; Roonwal, 1937). There is no positive evidence indicating that the ampullae give rise to the gonapophyses. Matsuda (1957) has also pointed out that the musculature associated with the eversible sacs and with the gonapophyses does not substantiate homology between the two structures. This misconception led Gustafson to conclude that the gonapophyses are homologous with not only the eversible sacs in pregenital segments in Thysanura, but further with the embryonic ampullae in Chilopoda and Onychophora. This view, while beautiful from the philosophical point of view, lacks scientific grounds. The eversible sacs in Thysanura are probably homologous with the coxal organs of some Diplopoda (Verhoeff, 1902).

Dupuis (1950) has tried to derive the male genitalia of all insects from the tenth abdominal appendages. His conclusions were reached solely on the basis of developmental studies of the male genitalia; female genitalia were ignored, as well as the morphology of the adult external genitalia of both sexes. If the male external genitalia are derived from the segmental limbs throughout all orders of insects, and if female genitalia are sternal in origin as has been strongly indicated above, we are faced with a great discrepancy which morphologists will be loath to accept. Therefore Dupuis' theory requires serious scrutiny.

Dupuis based his contention primarily on the study of embryonic and postembryonic development of the male genitalia in *Melanoplus differentialis* by Else (1934). This showed that the tenth abdominal appendage rudiments, after migration into the genital cavity formed above the ninth segment during development, give rise directly to the pseudosternite (definitive ninth sternum at the base of the paramere), paramere, and phallus. Else's study is perfect on its face, except that he did not mention whether the imaginal discs are formed or not. These were described many times by workers in the nineteenth century, and by Zander as the direct source of the genitalia. As already noted, this is one thing which led the present writer to suspect the precision of Wheeler's work. Since *Melanoplus* belongs to the Locustidae, the writer is inclined to suggest that the actual picture of the formation of the male genitalia might have been obscured, as Peytoureau and Heymons suspected in the case of *Xiphidium* (Tettigoniidae), by the precocious appearance of the imaginal discs which give rise to the male genitalia. Snodgrass (1937, p. 11) also indicated some doubts: "In Blattidae there may be three distinct lobes, and in Tettigoniidae as many as six in a young nymph. We may question, therefore, whether the two primary phallic lobes of Acrididae (Locustidae) are not independent outgrowths of the genital segment that might be confused with the simultaneously disappearing appendage rudiments of the tenth abdominal segment." In any case, Else's work is not free from doubt.

All other studies to which Dupuis took recourse in support of his contention are likewise subject to serious doubts and reinterpretations. Snodgrass (1941, pp. 5–6) admits that the concept of the origin of the phallic organ from the tenth abdominal segment cannot be carried over to holometabolous insects, since many of these have well developed appendages on the tenth segment of the larva that take no part in forming the genital organ whose rudiments are present, at the same time and in the same species, as a pair of small discs on the venter of the ninth segment. To avoid this difficulty Dupuis refers to a part of Graber's work (1890, pp. 702–705) where it was suggested that the appendages of the definitive tenth segment are actually those of the eleventh segment in Lepidoptera. But on pages 705–706 of the same paper Graber apparently indicates the presence of the tenth abdominal legs in Hymenoptera. Pryor (1951) in his extensive work covering the larval leg of Neuroptera, Trichoptera, and Lepidoptera, clearly indicates the presence of the tenth abdominal legs, and also shows that basal parts of the abdominal appendages are formed from the ninth segment in many species of Trichoptera. Dupuis regarded the work of Carrière and Burger (1897) on *Chalicodoma* as concordant evidence in support of his contention; one of these authors, Carrière, remarked (p. 340): "Never have I been able to recognize clearly more than two pairs of abdominal appendages, and only indeed on the third and fourth abdominal segments." Therefore, there are no embryonic rudiments whatever on the tenth segment which would give rise to the male genitalia.

Roonwal (1937) said in his work on *Locusta* (which was also cited by Dupuis) that the tenth abdominal segment shifts forward and fuses with the ninth, and that together they form the aedeagus and its ducts and ejaculatory ducts. Roonwal's work, however, indicates that the male genitalia are of appendicular origin but are derived from two segments, and thus does not lend perfect support for Dupuis' contention. Moreover, since the species Roonwal treated is a locustid, the same suspicion as to accuracy of observation can be entertained as for *Melanoplus* (Else, 1934).

The work of Sharif (1937) on the development of the flea *Xenopsyllus*, which too was cited by Dupuis in support of his contention, showed that the rudiments of the male external genitalia first appear in the third stage larva, on the ventral conjunctival membrane between the ninth and

tenth segments. In the prepupal stage a second pair of rudiments appears independently on the ninth venter, and gives rise later to the subgenital plates. The independent and discontinuous developments of two pairs of rudiments from the same segment led Sharif to conclude that one pair (the genitalia rudiments) should belong to the tenth segment, on the ground that if these two pairs represent biramous limbs the two parts of each should not have independent origin one after the other. If we substitute Heymons' theory for that of the limb origin of genitalia, Sharif's findings can be interpreted differently. Since the genitalia and appendages, according to Heymons, can arise independently in the same segment, the genitalia can be assigned to the ninth segment where Zander always found them. Qadri's works (1940, 1949), also cited by Dupuis, can be reinterpreted in the same manner as that of Sharif.

Dupuis also thought that the terminal ampullae which lie in the tenth abdominal appendages are closely associated with the formation of the male phallic organ. As was mentioned previously, the ampullae are later united with the ejaculatory duct or form the accessory gland. The ampullae and the appendage rudiments are quite different things. There is no evidence of any actual relationship between them, as Gustafson (1950) pointed out. A series of Heymons' works, cited by Dupuis as indirect evidence, cannot be used in support of his theory. In favor of Dupuis' contention, Ford's study (1923) on the musculature associated with the male genitalia in orthopteroid insects indicated that the pseudosternite belongs to the tenth segment, but this work did not refer to the nature, appendicular or otherwise, of the phallic organ.

It is apparent from the foregoing discussion that Dupuis' contention lacks enough supporting evidence to be accepted as a general principle. It will be noticed also that the works on species of Locustidae and Tettigoniidae always indicate that the male genitalia are appendicular in origin, while studies made on other insects do not. The same observation was made in the discussion of the female genitalia. Zander's studies (1900–1903) consistently showed that the phallic lobes arise from the hind margin of the ninth segment. In Mehta's account (1934) there is certainly nothing to suggest any possible relation of the primitive phallic lobes to the larval appendages of the tenth segment in Lepidoptera, and this is true also of D'Rozario's study (1942) on Hymenoptera.

Taking the female genitalia into consideration at the same time, the overall indication is that the tenth abdominal appendage rudiments have nothing to do with the formation of the male external genitalia. The contradictory evidence which has always been found in Locustidae and Tettigoniidae, specialized families of Orthoptera, is open to serious doubts, and has been variously questioned by Snodgrass (1937), Gustafson (1950), and the present writer in this paper.

Snodgrass (1937) surmised that the insect phallic organ is either an independent product of the genital integument around the mouth of the ejaculatory duct, or a product of the tenth abdominal appendages. This is really an honest impression that we get if we read the literature on male genitalia only. However, the similarity in the mode of development of the male genitalia and the ovipositor valvulae of the ninth segment (second and third valvulae) in the female, seems to suggest that in the two sexes they are homologous structures of the same segment.

CONCLUSION

From the foregoing discussion it is apparent that the weight of evidence regarding the origin of external genitalia of insects is more heavily in favor of Heymons' theory, and the overall indication is that the external genitalia have nothing to do with segmental limbs. Evidence contradictory to Heymons' theory has been found only in developmental studies on species of Tettigoniidae and Locustidae (Orthoptera), and has been questioned on various grounds by several workers. No evidence has been found in other groups of Orthoptera (such as Blattidae and Gryllidae) concordant with what has been reported for Locustidae and Tettigoniidae.

It should be recalled that the primitiveness of the pleurosternal region of the neuropteroid thorax was emphasized by Ferris (1940). Michener (1944) indicated that the male genital structures are more primitive in certain Neuroptera (e. g., *Agulla*) than in supposedly primitive Orthoptera. Matsuda (1957), as already noted, has shown that the female genitalia of *Agulla* can directly be homologized to a great extent with those of *Neomachilis* (Thysanura), both in external structures and associated musculature. The commonly or subconsciously accepted impression among entomologists that orthopteroid insects are standard insects possessing all primitive structures among pterygote forms is no longer tenable. Moreover, Heymons (1897a) showed that the gonapophyses in *Lepisma* (Thysanura), as in holometabolous insects, are quite independent from the appendage rudiments in origin. A few contradictory data from the embryology of certain orthopterous groups alone are hardly to be accepted as the basic principle, even if they are confirmed.

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NEW DATA ON THE BIOLOGY OF STILBOMETOPA IMPRESSA (BIGOT) AND LYNCHIA HIRSUTA FERRIS (DIPTERA: HIPPOBOSCIDAE)[1]

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Stilbometopa impressa (Bigot) and *Lynchia hirsuta* Ferris are ectoparasites of California quail. The biology of these hippoboscids is of special importance since these flies have been found to be vectors of *Haemoproteus lophortyx* O'Roke, a malarial parasite of California quail. O'Roke (1930) demonstrated that *L. hirsuta* was a vector of this malaria. Kadner (1941), Herman and Bischoff (1949) and Tarshis (1953, 1955) incriminated *S. impressa* also as a vector.

With the exception of Herman's paper (1944) on pupal development of *S. impressa*, little work has been done on the biology of the quail Hippoboscidae. The writer's investigations on the transmission of *H. lophortyx* to California quail by *S. impressa* and *L. hirsuta* netted much new data on the biology of these two ectoparasites, though mostly on *S. impressa*.

MATERIALS AND METHODS

The Hippoboscidae used in these investigations were obtained solely from *Lophortyx californica californica* (Shaw and Nodder), the Valley California Quail, and *Lophortyx californica brunnescens* Ridgway, the Coastal California Quail. Both quail are subspecies of *Lophortyx californica* (Shaw and Nodder), the California Quail, and it is quite difficult, except on very close examination, to differentiate between the two. For most purposes the two subspecies are so closely related that differentiation is not of great importance. Details on these quail will be found in the works by Grinnell (1931), Grinnell and Miller (1944) and Emlen and Glading (1945).

The two species of hippoboscids found on the California quail belong to the subfamily Ornithomyiinae and to the genera *Stilbometopa* and *Lynchia*. *Stilbometopa impressa* (Fig. 1) is the larger of the two species having a wing length of 8 to 9 mm. *Lynchia hirsuta* (Fig. 2) has a wing length of 4.5 to 5.5 mm. For details on the taxonomy of these flies see Bequaert (1953, 1954, 1955 and 1957).

During the years 1948 to 1952, 2 to 5 weeks of each summer were spent trapping quail and collecting the flies from them for colonizing purposes. Collections of quail were made twice a day from the traps (morning and evening). The trapped quail were placed in fly-proof holding cages and brought back to the field station where in fly-proof, portable insectaries the flies were recovered from each quail. The flies were placed into shell vials 24 mm. wide by 95 mm. long and then plugged with screened corks. Wooden racks were used to hold the shell vials. If the flies were to be transported on quail from the field to Berkeley they were later re-placed on the quail, but if they were to be transported in a cold temperature cabinet they were left in the shell vials. For further details on insectaries, transporting live flies, traps and trapping quail see Tarshis (1952, 1953, 1954 and 1956).

The quail (louse) flies were always maintained in the laboratory on quail kept in fly-proof cages. Bird cages of several designs and sizes were used, but a 12⅞ by 15¼ by 15¼-inch, wood framed, screened covered cage was found most suitable (Tarshis, 1954). Larger cages may be used if it is essential to keep more than one or two birds in a cage, but this is not advisable if the quail are to harbor flies. Quail are easily excited; the more birds in a cage the greater the resultant commotion, which causes the flies to leave the birds and makes them easier prey for the quail.

To minimize fly losses the quail were always "hyponotized" when flies were introduced onto them (Tarshis, 1953, 1954). Just placing the opened fly vial in the cage or merely dropping the flies from the vial onto the bird in anticipation of the flies establishing themselves on the quail was not satisfactory as the flies were most often eaten or trampled on before they could become established.

Each puparium was placed in a separate rearing vial. The same size shell vials were used for rearing the puparia as were used for field collected flies. The majority of the puparia were reared in incubators built by the author (Tarshis, 1953).

Colonies of *S. impressa* were more readily maintained than those of *L. hirsuta*, a difference attributed mainly to the ease with which quail could capture the smaller fly and the difficulty they had in catching the larger fly.

RESULTS AND DISCUSSION

Geographical Distribution of Quail Hippoboscidae in California

The writer's findings indicate that there may be distinct differences in the geographical distribution of *S. impressa* and *L. hirsuta* within the

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State of California. In the ten trapping areas of this study (Fig. 3) there were seven in which one of the two species of flies predominated, one area in which both species were present in about equal numbers, and two areas in which neither fly was found (Table 1). No flies have ever been recorded on quail in San Francisco County and none were found during the current studies. In Alameda County no flies were taken during the writer's trappings, but flies have been recorded in this area. Their absence this time was due no doubt to the fact that trapping was done very late and very early in the season, when there is a paucity of flies in most areas.

Although 165 quail were trapped at the Hunter Liggett Military Reservation (Monterey County), the data on the distribution in this area have not been considered as conclusive as the size of the trapping indicates they should be, since the number of quail trapped was such a small percentage of the tremendous number of quail to be found in the area.

Many more trappings will have to be made throughout the state before it will be known definitely if the indicated geographical division of species exists or not.

TABLE 1

HIPPOBOSCIDAE OBTAINED FROM TRAPPED CALIFORNIA QUAIL

LOCALITIES (FROM NORTH TO SOUTH)	YEAR	QUAIL TRAPPED	FLIES TAKEN	
			S. impressa	*L. hirsuta*
Chiles Ranch (Napa Co.)	1948	326	8	22
	1949	268	7	247
Lafayette (Contra Costa Co.)	1950	6	0	1
San Pablo Dam (Contra Costa Co.)	1949	45	2	26
Berkeley (Alameda Co.)	1949	27	0	0
San Francisco (San Francisco Co.)	1949	23	0	0
Watsonville (Santa Cruz Co.)	1949	39	3	1
Bitterwater (San Benito Co.)	1948	191	148	101
	1949	456	299	255
	1952	550	283	134
Hunter Liggett (Monterey Co.)	1951	165	30	159
Shandon (San Luis Obispo Co.)	1950	388	326	4
	1951	160	159	2
	1952	442	282	1
Cedar Canyon (Kern Co.)	1949	227	321	60
Totals		3313	1828	1016

New Collection Data on Quail Hippoboscidae Taken in California

Stilbometopa impressa. Bitterwater, 15 miles S. E. of King City, San Benito County, on *Lophortyx californica californica*, Aug. 23, 25, 27, 1948 (Calif. Dept. Fish and Game); Sept. 21, 22, 1948 (Tarshis, Herman and Selleck); Sept. 27, 1948 (Calif. Dept. Fish and Game); Aug. 27, 28, 29, 30, 1949 (Tarshis and Tarshis); Sept. 27, 28, 29, 1949 (Tarshis and MacGregor); Aug. 6, 7, 8, 9, 10, 11, 12, 13, 1952 (Tarshis, Furman, Rudnick, Rohrbacker and Berg). Chiles Ranch, Chiles Valley, about 15 miles N. E. of Yountville, Napa County, on *Lophortyx c. californica*, Nov. 4, 11, 13, 16, 1948 (Tarshis, Herman and Hightower); June 13, 1949 (Tarshis and Hightower); July 14, 15, 27, 1949 (Tarshis and Hightower); Aug. 18, 1949 (Tarshis and Hightower). Watsonville, Santa Cruz County, on *Lophortyx californica brunnescens*, Sept. 9, 1949 (Tarshis and Hightower). Cedar Canyon, Cook Spring, Kern County, on *Lophortyx c. californica*, Sept. 21, 22, 23, 1949 (Tarshis, Azevedo and Hightower); Oct. 17, 18, 19, 20, 21, 1949 (Tarshis, Azevedo and Hightower). Hunter Liggett Military Reservation, Jolon, Monterey County, on *Lophortyx c. californica*, Sept. 20, 1948; Nov. 24, 1948; Dec. 8, 13, 1948; Sept. 16, 22, 23, 26, 28, 1949; Oct. 1, 2, 3, 4, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 29, 1949; Nov. 2, 7, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 26, 30, 1949; Dec. 5, 31, 1949; Jan. 1, 1950 (Calif. Dept. Fish and Game); Sept. 17, 18, 19, 20, 21, 22, 1951 (Tarshis and Rudnick). McMillan Ranch, about 15 miles N. E. of Shandon, San Luis Obispo County, on *Lophortyx c. californica*, Aug. 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 1950 (Tarshis and Koobs); Oct. 11, 12, 13, 14, 15, 16, 1950 (Tarshis); Aug. 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 1951 (Tarshis and Tarshis); Aug. 25, 26, 27, 28, 29, 30, 31, 1952 (Tarshis and McMillan); Sept. 1, 2, 3, 4, 5, 6, 7, 1952 (Tarshis and McMillan).

Lynchia hirsuta. Bitterwater, San Benito County, on *Lophortyx californica californica*, Aug. 23, 25, 1948 (Calif. Dept. Fish and Game); Sept. 21, 22, 1948 (Tarshis, Herman and Selleck); Sept. 27; Nov. 24, 1948 (Calif. Dept. Fish and Game); Aug. 27, 28, 29, 30, 1949 (Tarshis and Tarshis); Sept. 27, 28, 29, 1949 (Tarshis and MacGregor); Sept. 21, 1950 (Calif. Dept. Fish and Game); Aug. 6, 7, 8, 9, 10, 11, 12, 13, 1952

(Tarshis, Furman, Rudnick, Rohrbacker and Berg), Chiles Valley, Chiles Ranch, Napa County, on *Lophortyx c. californica*, Nov. 5, 6, 7, 8, 9, 10, 11, 1948 (Tarshis, Herman and Hightower); June 8, 22, 30; July 14, 15; Aug. 18, 1949 (Tarshis and Hightower). San Pablo Dam Area, Orinda, Contra Costa County, on *Lophortyx californica brunnescens*, June 21; Oct. 30; Nov. 3, 1949 (Tarshis and Hightower). Watsonville, Santa Cruz County, on *Lophortyx c. brunnescens*, Sept. 9, 1949 (Tarshis and Hightower). Cedar Canyon, Cook Spring, Kern County, on *Lophortyx c. californica*, Sept. 21, 22, 23; Oct. 17, 18, 19, 20, 21, 1949 (Tarshis, Azevedo and Hightower).

trappings of quail from January to May revealed a complete absence of flies. During the first week in June *L. hirsuta* were taken from quail, and on the 13th of June *S. impressa* were found on quail. At Shandon, San Luis Obispo County, *S. impressa* was found as early as April and as late as mid-November. *Lynchia hirsuta* is not generally found at any time at Shandon. A few *S. impressa* have been taken from quail on the Hunter Liggett Military Reservation, Monterey County, early in January.

In most areas the greatest number of flies (the species depending on the trapping area) is generally found during August, September and the

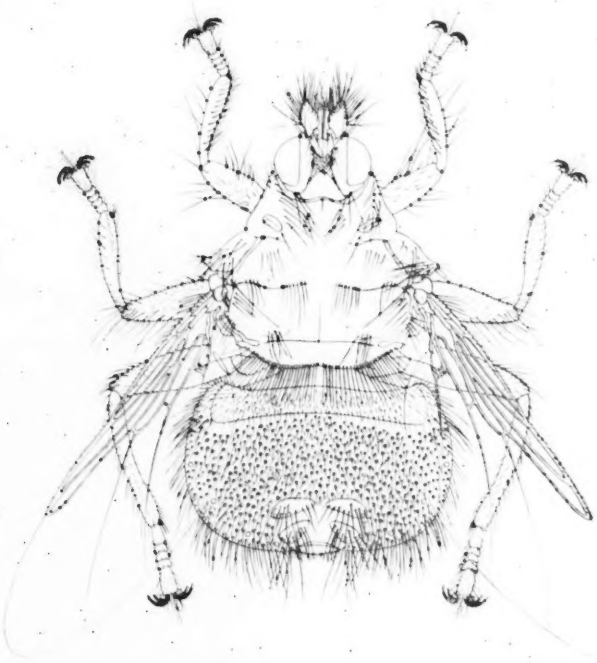

FIG. 1. *Stilbometopa impressa* (Bigot) (after Bequaert, 1955).

McMillan Ranch, Shandon, San Luis Obispo County, on *Lophortyx c. californica*, Aug. 7, 13, 14, 16, 1950 (Tarshis and Koobs); Aug. 24, 1951 (Tarshis and Tarshis); Sept. 2, 1952 (Tarshis and McMillan). Lafayette, Contra Costa County, on *Lophortyx c. brunnescens*, Nov. 7, 1950 (Tarshis). Hunter Liggett Military Reservation, Jolon, Monterey County, on *Lophortyx c. californica*, Sept. 20; Dec. 8, 1949; Sept. 16, 22, 23; Oct. 1, 3, 11, 13, 18, 19, 22, 23; Nov. 12, 14, 17, 19, 1949 (Calif. Dept. Fish and Game); Sept. 17, 18, 19, 20, 21, 22, 1951 (Tarshis and Rudnick).

Months of Year Hippoboscidae Taken from Quail

At Chiles Ranch, Napa County, sporadic

first two weeks in October. After that, fly populations begin to decrease, and in most areas the flies completely disappear by the end of the year. The increase in the fly populations in August appears to be correlated with the development of the quail. Usually by August, when the greatest number of flies are found, the first-hatched broods of quail are fairly well grown and the last broods have reached about 10 weeks of age.

Number of Flies Taken from Each Trapped Quail

Whenever time permitted the writer kept complete records on the number, species and sexes of the flies found on the individual quail. Records

were kept on 1665 trapped quail from which 861 *S. impressa* and 506 *L. hirsuta* were taken. Only 78 of the birds harbored both species of fly at the same time. The data concerning the number of flies taken from these trapped quail will be found in Table 2.

The majority of the trapped quail were found to harbor only one fly each. The next most common occurrence was the harboring by each quail of two flies of the same species. Few birds harbored more than a total of four flies each, though on rare occasions a quail was found with five to eight flies. No bird was ever found harboring more than eight flies. Quail under four weeks of age were found to harbor virtually no flies.

Sex Ratio of Quail Hippoboscidae

Of a total of 1828 *S. impressa* taken from trapped quail 667 were males (36.48 per cent) and 823 were females (45.02 per cent); the sex of 338 *S. impressa* adults (18.49 per cent) was not determined. Of a total of 1016 *L. hirsuta* taken from trapped quail 245 were males (24.11 per cent) and 341 were females (33.56 per cent); the sex of 430 *L. hirsuta* adults (42.32 per cent) was not determined.

Of 1533 *S. impressa* adults reared in the laboratory 782 were males (51.01 per cent) and 751 were females (48.99 per cent). From a total of 193 *L. hirsuta* adults reared in the laboratory 94 were males (48.70 per cent) and 99 were females (51.30 per cent).

Search for Stilbometopa impressa Puparia in the Field

Though the author sought *S. impressa* puparia in the field none were ever found. The majority of the searches were conducted in the shaded, densely shrubbed loafing areas in which the quail spent the major portion of each day during the mid-summer and early fall months. The author found that the hours for the majority of depositions were coincident with the quail loafing hours, and that the flies left the quail to deposit their prepuparia. Therefore, it was concluded that the majority of prepuparia must be deposited in or very near the loafing areas. However, whenever traps were being set or trapped quail were being collected a search was made for prepuparia in the trapping areas.

Each time that a search of a loafing area was conducted the ground under the shrubbery was thoroughly raked and the loose earth sifted through a specially constructed, No. 16 mesh, screen cloth sifter to be sure that no prepuparia or puparia had escaped detection during the raking. None was ever found, diligent though the searches were, which leads one to wonder just where or how they could be so well concealed. The possibilities that they might be affixed to shrubbery or buried in the ground seem very remote as *S. impressa* prepuparia never bore any trace of an adhesive residue and the

TABLE 2

NUMBER OF FLIES TAKEN FROM TRAPPED QUAIL

1665 Quail trapped (includes each bird each time it was trapped).

746 Quail harbored flies (includes each bird each time it was trapped).

612 Quail harboring flies were taken in traps one time only and 67 quail were taken twice (data on flies taken on first trapping only).

398 Quail harbored *S. impressa*

243 Quail harbored 1 fly each
97 " " 2 flies each
32 " " 3 flies each
19 " " 4 flies each
4 " " 5 flies each
1 " " 6 flies
2 " " 7 flies each

203 Quail harbored *L. hirsuta*

120 Quail harbored 1 fly each
44 " " 2 flies each
19 " " 3 flies each
6 " " 4 flies each
10 " " 5 flies each
2 " " 6 flies each
1 " " 7 flies
1 " " 8 flies

78 Quail harbored both *S. impressa* and *L. hirsuta*

28 Quail harbored 1 fly of each species.
28 Quail harbored 3 flies each
15 Quail harbored 1 *S. impressa* and 2 *L. hirsuta* each
8 Quail harbored 2 *S. impressa* and 1 *L. hirsuta* each

15 Quail harbored 4 flies each
4 Quail harbored 1 *S. impressa* and 3 *L. hirsuta* each
7 " " 3 *S. impressa* " 1 *L. hirsuta* each.
4 " " 2 *S. impressa* " 2 *L. hirsuta* each

5 Quail harbored 5 flies each
1 " " 2 *S. impressa* and 3 *L. hirsuta*
1 " " 3 *S. impressa* " 2 *L. hirsuta*
3 " " 4 *S. impressa* " 1 *L. hirsuta* each

3 Quail harbored 6 flies each
2 Quail harbored 3 *S. impressa* and 3 *L. hirsuta* each
1 " " 4 *S. impressa* " 2 *L. hirsuta*

3 Quail harbored 7 flies each
1 Quail harbored 2 *S. impressa* and 5 *L. hirsuta*
1 " " 3 *S. impressa* " 4 *L. hirsuta*
1 " " 1 *S. impressa* " 6 *L. hirsuta*

1 Quail harbored 8 flies
1 Quail harbored 6 *S. impressa* and 2 *L. hirsuta*

67 Quail harboring flies were taken in traps twice (data on flies taken on second trapping only)

58 Quail harbored *S. impressa*
43 Quail harbored 1 fly each
12 " " 2 flies each
2 " " 3 flies each
1 " " 4 flies

5 Quail harbored *L. hirsuta*
3 Quail harbored 1 fly each
1 " " 2 flies
1 " " 3 flies

4 Quail harbored both *S. impressa* and *L. hirsuta*
3 Quail harbored 1 *S. impressa* and 1 *L. hirsuta* each
1 " " 1 *S. impressa* and 3 *L. hirsuta*

deeper soil in the raked areas was so hard and dry at that time of year that it seems most unlikely the flies could have dug deeply enough to bury their prepuparia. *Lynchia hirsuta* puparia were never actively sought in the field.

Flight and Running Pattern of Quail Hippboscidae

On several occasions the writer was able to observe *S. impressa* escaping from quail while the quail were being removed from the traps. *Lynchia hirsuta* were not observed leaving the birds during this operation.

Both species of flies were observed flying off the quail when the birds' feathers were ruffled to dislodge the flies. Whether the flies left of their own volition or were forced off, their flight pattern was always the same. They rarely flew more than a few inches at a time, always darted directly toward a solid surface—screening, the frame of the trap, or even the worker—and then remained motionless for sometime. If disturbed, as when one is trying to capture them, the flies would more often run than fly to escape capture.

Neither species of fly was ever observed flying from one part of a bird's body to another. Rather they ran very quickly over and under the feathers in a very distinctive zig-zag pattern. This same pattern was followed when the flies ran on screening or any other object. They moved so rapidly and in such a peculiar manner it was sometimes most difficult to capture them on the quail, and for this reason the quail's feathers were always ruffled for several minutes.

Though *S. impressa* and *L. hirsuta* flew onto the author and co-workers on innumerable occasions, and even became trapped in hair or beneath clothing any number of times, no bites were experienced.

Longevity of Quail Hippoboscidae

The writer found that both *S. impressa* and *L. hirsuta* when removed from quail survived for only 3 to 4 days at room temperature. This short survival period does not appear to be due to starvation, but rather to the extreme change in microclimate since large quantities of blood were found in the diverticula and guts of many of the flies that died. The writer has kept newly-emerged *S. impressa* alive in the laboratory for as long as 14 days at room temperature (65° F.), but 7 to 8 days was the more usual life span at this temperature. At 78.0° F. *S. impressa* generally survived 6 to 7 days. Newly-emerged *L. hirsuta* have been kept alive for 7 to 8 days at room temperature (65.0° F.) and 5 to 6 days at 78° F. All newly-emerged flies were unfed. This resistance to starvation by the newly-emerged flies is undoubtedly an important factor in the field where these ectoparasites emerge from the puparia off the host and have to survive without food until a host can be found. At 40° F. fed *S. impressa* could be held for 7 days and fed *L. hirsuta* for 8 days off their host. Under laboratory conditions *S. impressa* were kept alive on quail for periods ranging from 1 to 162 days and *L. hirsuta* from 2 to 77 days.

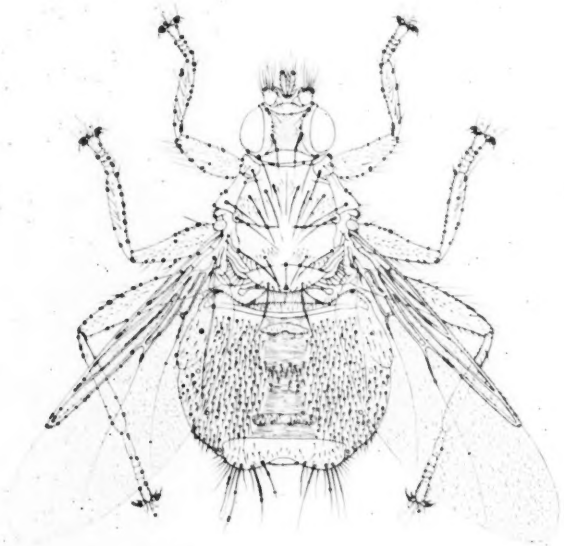

FIG. 2. *Lynchia hirsuta* Ferris (after Bequaert, 1955).

Mating of Quail Hippoboscidae

Stilbometopa impressa have never been observed *in copula*; however, experimental evidence indicates that once females are fertilized they are fertile for life. In one experiment a newly-emerged female and a newly-emerged male *S. impressa* were placed together on a quail for three days. On the third day the male fly was removed and six days later the female fly deposited her first prepuparium; thereafter, she deposited a prepuparium every six days. This experiment was repeated a number of times.

FIG. 4. Ventral view of gravid *Stilbometopa impressa* (Bigot) showing unique attachment of prepuparium just prior to being deposited.

Lynchia hirsula was observed *in copula* many times. When gravid *L. hirsula* were flushed from quail, male flies were often found clinging to the dorsal surfaces of the females. Whenever the sexes were taken together the female was always about to deposit a prepuparium. The male fly clung to the female by securing its second pair of legs around her waist and its third pair of legs around her abdomen. The female's wings were widely separated so that, despite the male's attachment, she was able to fly from the bird to the place where she wished to deposit her prepuparium. After deposition of the prepuparium copulation occurred, then the female flew with the male to another bird.

Gestation Period of Stilbometopa impressa

The time required for each stage of gestation is not known, but the total length of time was found to be about six days when the temperature averaged above 48° F. The period increased to 7 to 10 days when the temperature averaged below 48° F. The gestation period was determined by the time lapses between prepuparial depositions.

Records of prepuparial depositions every six days were obtained innumerable times on individual female *S. impressa*. When groups of 2 to 14 females were placed together in one cage the prepuparial data also showed 6-day lapses between depositions when the temperatures averaged above 48° F. Some of these experimental findings are shown in Table 3.

The flies whose depositions were recorded were all kept outdoors. The average monthly mean temperatures during these deposition studies ranged from 48.9° F. to 64.9° F. except in January, which averaged 48.0° F. During January prepuparial depositions occurred every seven days; however, a few depositions occurred at 10-day intervals.

The gestation period for *L. hirsula* has not been determined, but from the few observations the author was able to make it appears to be about the same as for *S. impressa*.

The number of prepuparia that a female of either species generally deposits in a lifetime has not been determined. As will be seen in Table 3, on occasion a female *S. impressa* did deposit as many as 11 prepuparia; but on many other occasions females deposited from 3 to 7.

Deposition of Prepuparia by Quail Hippoboscidae

Three distinct stages in the deposition of a prepuparium by *S. impressa* were observed. The first two stages occurred while the fly was still on the quail and the third stage occurred after the fly had left the bird. The flies always left the birds to deposit their prepuparia and they most often made their depositions in the shaded or dark tray of the quail cage.

Stage I. During this first fifteen minute stage of deposition one third of the prepuparium, including the prominent posterior stigmatic plate, is ejected by the female fly. The prepuparium when first ejected has a fairly hard integument and is shiny and creamy yellow except for the intensely black stigmatic lobes. It gradually changes to a light amber color.

Stage II. When the prepuparium has changed to the light amber color the fly ejects approximately another third (or a little more) of the prepuparium. It is now shinier in appearance and the integument is slightly tougher than during Stage I. The appearance of the prepuparium at this stage, protruding out of the vaginal opening, reminds one of the ootheca of

certain cockroaches (Fig. 4). The prepuparium is so securely attached that the female fly can fly about for quite a long time without dropping it. The prepuparium now changes from a light amber to a true amber color. This stage lasts about 30 minutes.

Stage III. Once the amber color of the prepuparium is attained the female fly leaves the bird and flies to the site where she will deposit the prepuparium. The prepuparium retains the same color during this ten to fifteen minute stage.

After the prepuparium is dropped it continues to undergo the color changes described in Table 4. When the shiny ebony color is reached and the integument has become completely chitinized the prepuparium has become a *puparium*.

develop further. During these studies 89 prematurely deposited larvae were collected. No black puparia or even dark brown prepuparia were ever seen attached to the females or being deposited. In 138 recorded observations (Table 5) only 8 attached prepuparia were darker than amber. *Stilbometopa impressa* prepuparia have been found to be quite dry and to have no adhesive substances on their outer surfaces. The normal, fully formed puparium is 5.3 to 5.5 mm. in length, 4.9 to 5.1 mm. at its greatest width, and about 3.5 mm. in thickness.

The female of *L. hirsuta* normally deposits a creamy white prepuparium measuring 2.2 mm. in length, 1.8 mm. in width, and 1.4 mm. in thickness. Unlike that of *S. impressa*, this is

TABLE 3

DEPOSITION OF PREPUPARIA BY *Stilbometopa impressa*

QUAIL CAGE	FLIES	DATES OF DEPOSITION	TOTAL PREPUPARIA DEPOSITED
No. 16	1 and 2	5-23-49, 5-29-49, 6-4-49, 6-10-49, 6-16-49, 6-22-49, 6-28-49	7 each
No. 59	1 and 2	9-24-49, 9-30-49, 10-6-49, 10-12-49, 10-12-49, 10-24-49, 10-30-49	7 each
	3 to 6	9-24-49, 9-30-49, 10-6-49, 10-12-49	4 each
	7 to 10	9-25-49, 10-1-49, 10-7-49, 10-13-49, 10-19-49,	5 each
	11 to 14	9-25-49, 10-1-49, 10-7-49, 10-13-49	4 each
No. 60	1 to 5	10-2-49, 10-9-49, 10-14-49, 10-20-49, 10-26-49	5 each
No. 71	1	11-29-49, 12-5-49, 12-11-49, 12-17-49, 12-23-49, 12-29-49, 1-4-50, 1-10-50, 1-16-50, 1-23-50 (7 days), 1-30-50 (7 days)	11
No. 2	1 to 3	9-18-52, 9-24-52, 9-30-52	3 each
	4 to 6	9-19-52, 9-25-52, 10-1-52	3 each
	7 to 9	9-20-52, 10-26-52, 10-2-52	3 each
No. 23	1 and 2	12-3-52, 12-9-52, 12-15-52, 12-21-52, 12-27-52, 1-23-53	6 each
	3 and 4	12-6-52, 12-12-52, 12-18-52, 12-24-52, 12-30-52, 1-5-53	6 each
	5 and 6	12-11-52, 12-17-52, 12-23-52, 12-29-52, 1-4-53	5 each
	7 and 8	12-19-52, 12-25-52, 12-31-52, 1-6-53	4 each
	9 and 10	12-22-52, 12-28-52, 1-3-53, 1-9-53	4 each

The $11\frac{1}{4}$ hour color change period recorded in Table 4 was average for prepuparia deposited in Berkeley during most months of the year. On very cold days, however, the color changes took as long as 36 hours, and on extremely warm days the color changes occurred in as few as 4 or 5 hours.

Under abnormal conditions the flies do deposit prepuparia instantaneously. Female flies that are disturbed 1 or 2 hours prior to the time for normal deposition will quickly deposit prepuparia that are creamy white with shiny, hard integuments. These prepuparia will continue to change color and develop into normal puparia, eventually producing normal adult flies. Should the gravid female be disturbed a day or so before she is ready to deposit the prepuparium, she will abort a dull white, wrinkled larva which will fail to

deposited all at once rather than in stages. Like *S. impressa*, the *L. hirsuta* female always leaves the quail and seeks a dark or shaded spot, such as the tray of the cage, for prepuparial deposition. The prepuparium of this species has an adhesive coating on its outer surface, and many have been found adhering to the walls of the rearing vials when, for various reasons, gravid females were placed in the vials. The series of color changes and patterns that the *L. hirsuta* prepuparium undergoes after it leaves the uterus of the female is listed in Table 6.

The complete color and pattern change for this prepuparium of *L. hirsuta* took five hours, which is average for the prepuparia of this species during the summer, fall, and early winter months in Berkeley. Variations in the time required for development of these changes at extremely high

and low temperatures were not observed, but it is probable that the transition is affected by temperature in the same manner as in prepuparia of *S. impressa*. *Lynchia hirsuta* was never observed depositing prepuparia prematurely, and all prepuparia deposited by this species developed normally to puparia.

The author observed that the majority of prepuparial depositions of *S. impressa* occurred between 11 a. m. and 5 p. m., with the greatest number occurring between 1 p. m. and 2 p. m. When the weather was exceptionally cold, a small number of depositions occurred after 5 p. m., and when the weather was exceptionally warm a small percentage took place before 11 a. m.

TABLE 4

COLOR CHANGES OF A PREPUPARIUM AFTER DEPOSITION BY A FEMALE *Stilbometopa impressa*

HOUR OF OBSERVATION	TIME AFTER DEPOSITION (HRS)	COLOR
12:15 P. M.	0	Amber
12:45 P. M.	½	Deep Amber
1:15 P. M.	1	Reddish-Amber
1:45 P. M.	1½	Reddish-Orange
2:15 P. M.	2	Dark Reddish-Orange
2:45 P. M.	2½	Dark Amber
3:30 P. M.	3¼	Very Dark Amber
4:00 P. M.	3¾	Deep Reddish-Brown
4:45 P. M.	4½	Edges commencing to turn black, center remaining deep reddish brown
5:15 P. M.	5	Reddish-Black
6:30 P. M.	6¼	Darker Reddish-Black
7:15 P. M.	7	Reddish color disappearing
8:30 P. M.	8¼	Becoming very dark, but still has reddish tinge
9:30 P. M.	9¼	Deeper black, reddish color almost gone
10:30 P. M.	10¼	Black, except for one or two reddish-black spots
11:30 P. M.	11¼	Deep shiny black

Data on *L. hirsuta* are not as complete as those on *S. impressa*, but it was found that gravid females generally deposited their prepuparia between the hours of 11 a. m. and 3 p. m.

Pupal Development at Various Temperatures

During the early experimental rearing of Hippoboscidae the writer attempted to incubate puparia of both *S. impressa* and *L. hirsuta* at 95.9° F., the temperature O'Roke (1930) reported using for rearing a puparium of *L. hirsuta*. The writer placed 14 puparia of *S. impressa* and 6 of *L. hirsuta* in an incubator set at 95.9° F., with a relative humidity of approximately 35 percent. After 85 days no adults had emerged. The puparia were opened between the 85th and the 93rd days, and were found to be completely desiccated. Another group of 22 puparia of *S. impressa* were placed in an incubator set at 95.9° F., but with a relative humidity of about 50 percent. Nine flies emerged in 30 to 37 days, but all were deformed. The remaining 13 puparia were opened and were found to be completely desiccated.

After the failure to obtain flies from puparia at a temperature of 95.9° F., experimentation showed that normal adult flies could be obtained from puparia incubated at 78° F. with a relative humidity of about 38 percent. A total of 871 *S. impressa* puparia incubated under these conditions yielded adult flies in 24 to 53 days. The majority of the flies emerged in 29 to 46 days, and the greatest number emerged in 37 days. When 189 *L. hirsuta* puparia were kept at this same temperature and humidity adult flies emerged in 17 to 32 days. The majority of the adults emerged in 27 to 30 days and the greatest number in 28 days.

Of 146 *S. impressa* puparia incubated at 82.0° F. with a relative humidity of about 41 percent, the majority of adults emerged in 34 to 38 days with the greatest number of emergences occurring in 35 days.

TABLE 5

COLOR AND TIME OBSERVATIONS ON PREPUPARIA ATTACHED TO FEMALE OF *Stilbometopa impressa*

HOUR OBSERVED	COLORS OBSERVED				
	Creamy White	Lemon Yellow	Amber	Red Amber	Dark Amber
10:00 A.M.	3	2	6		
11:00 A.M.	11	13	23		
Noon	1		8		
1:00 P.M.	1	9	24		
2:00 P.M.	2	2	21		
3:00 P.M.			3	1	
4:00 P.M.			1	1	4
5:00 P.M.				1	
6:00 P.M.					1
Totals	18	26	86	3	5

At 84.0° F. with an approximate humidity of 41 percent, 136 adult *S. impressa* emerged from puparia in 30 to 36 days. The greatest number emerged in 31 days. At 90.0° F. with a relative humidity of about 41 percent, 14 *S. impressa* emerged as adults from puparia in 27 to 31 days with the majority emerging in 28 and 29 days.

Adults emerged in 106 to 208 days from 84 *S. impressa* puparia kept at room temperature (average temperature was 58.8° F.). Five *L. hirsuta* emerged as adults in 46 to 195 days when these puparia were held at this same room temperature.

Experiments in which puparia of *S. impressa* and *L. hirsuta* were exposed to outdoor temperatures were conducted in Berkeley during 1948 and 1949. The monthly mean minimum-maximum temperatures for January to December 1948 and 1949 were as follows:

BERKELEY TEMPERATURES DURING 1948 AND 1949, °F

MONTHS	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.
						1948						
Minimum	36	34	36	40	40	50	54	55	52	52	46	40
Maximum	70	68	73	70	75	88	72	73	73	71	65	52
						1949						
Minimum	35	40	46	47	51	54	53	55	55	50	51	41
Maximum	50	54	61	67	67	71	69	72	75	70	78	56

Thirty-five *S. impressa* puparia were placed outdoors between October 8 and 29, 1948. Since no adults emerged after a period of 120 to 141 days, six puparia were taken from this group and placed in a 78.0° F. incubator to determine if they were still viable. Twenty-eight days later two adult flies emerged and four more adults emerged two days later. After the puparia had been outdoors for a period of 205 to 226 days, another puparium was taken from the group and placed in the 78.0° F. incubator. Twenty-eight days later a normal fly emerged.

After a total of 337 to 358 days the remaining 28 puparia still failed to yield adult flies. These puparia were opened and found to contain perfectly formed flies, which shows that puparia can survive long periods of time when kept at comparatively low temperatures.

Four *L. hirsuta* puparia kept outdoors with the *S. impressa* puparia yielded adult flies in 182 to 269 days. Limited though this experiment was, it seems to indicate that *L. hirsuta* also can survive long periods of storage at comparatively low temperatures. It is quite probable that puparia deposited by both species of flies late in the season overwinter as puparia and emerge as adult flies the following year when temperatures rise.

SUMMARY

From a total of 3313 quail trapped in ten localities in California between 1948 and 1952, 1828 *Stilbometopa impressa* (Bigot) and 1016 *Lynchia hirsuta* Ferris were taken. The majority of the trapped quail harbored only one fly each. The next most common finding was the harboring by each bird of two flies of the same species. Few birds harbored more than four flies each, but on rare occasions a quail was found with 5 to 8 flies; 78 quail harbored both species of flies.

The peak period for taking quail Hippoboscidae in California is from the first of August through the second week in October. All attempts to find puparia of *S. impressa* in the field met with failure.

Gravid females of *S. impressa* deposit as many as 11 prepuparia at intervals of six days when the prevailing temperature is 48° F. or above. When the temperature is below 48° F. depositions occur at 7- to 10-day intervals.

Deposition of prepuparia by *S. impressa* occurs

TABLE 6

COLOR AND PATTERN CHANGES OF A *Lynchia hirsuta* PREPUPARIUM AFTER DEPOSITION

HOUR OF OBSERVATION	TIME AFTER DEPOSITION	COLOR AND PATTERN CHANGES
12:30 P.M.	0	Creamy white (just being deposited).
1:05 P.M.	35 Minutes	Prepuparium changing to gray-white color; faint gray horizontal lines are discernible, but exact number cannot be determined. Stigmatic plate grayish-white.
1:15 P.M.	45 Minutes	Horizontal lines are now more prominent, on close observation ten can be seen. The stigmatic plate is darkening.
1:30 P.M.	60 Minutes	The ten horizontal lines are now prominent and black. The original white-gray background color of the prepuparium itself is now starting to turn yellow-amber color.
2:00 P.M.	90 Minutes	The horizontal black lines are widening, leaving narrow yellow-amber stripes.
3:00 P.M.	150 Minutes	The yellow-amber stripes are darkening and narrowing down to the very fine stripes which finally become the characteristic lines of the puparium. The original black lines have widened and cover the major portion of the prepuparium.
5:30 P.M.	300 Minutes (5 Hours)	The prepuparium has now completed the color change and is a deep mahogany on which are superimposed ten amber colored lines—three wide lines at the posterior, three wide lines at the anterior and four equally spaced lines in the center. It is now a puparium.

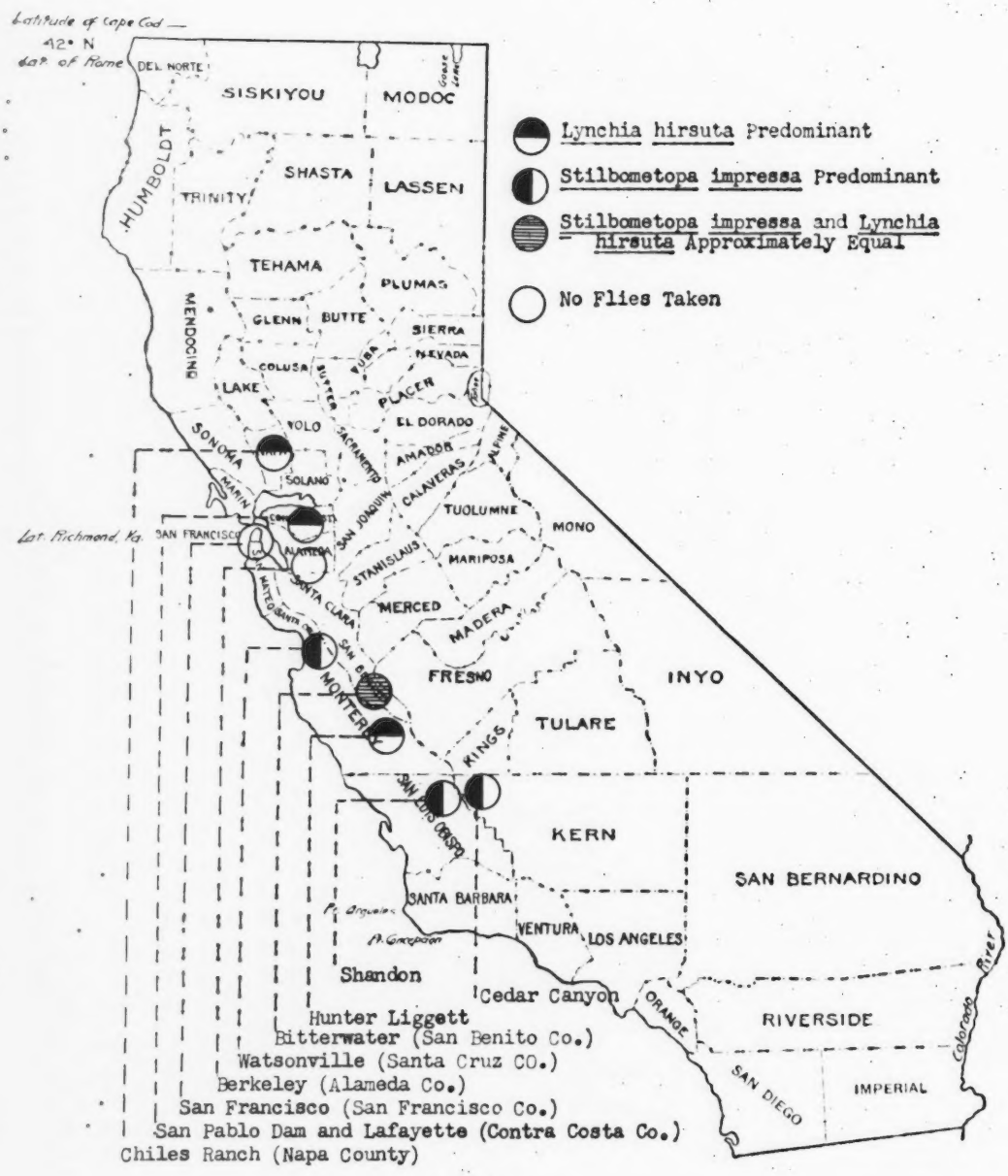

FIG. 3. Distribution of quail hippoboscids taken by the writer in the State of California.

in three distinct stages. The first two stages occur while the fly is still on the quail, and the third stage occurs after the fly has left the bird to deposit the prepuparium. It generallly takes about $11\frac{1}{4}$ hours for the newly deposited prepuparium to go through the complete color transition from amber to shiny black and to become a puparium. The prepuparium of *L. hirsuta* is deposited all at once; it generally takes about five hours for the newly deposited prepuparium to go through the complete color transition from creamy white to deep mahogany and to become a puparium.

The majority of prepuparial depositions of *S. impressa* occur off the bird between 11 a. m. and 5 p. m., with the maximum number of depositions occurring between 1 p. m. and 2 p. m. Gravid females of *L. hirsuta* also leave the birds to deposit their prepuparia, and deposition occurs between the hours of 11 a. m. and 3 p. m.

Experiments with puparia of *S. impressa* kept at various constant temperatures revealed that at 78.0° F. the greatest number of adult flies emerge in 37 days. At 82.0° F. the greatest number of adults emerge in 35 days and at 84.0° F. most adults emerge in 31 days. At 90.0° F. adults emerge in 28 and 29 days. At 78.0° F. adults of *L. hirsuta* emerge in 28 days.

Adults of *S. impressa* emerge from puparia in 106 to 208 days when kept at a room temperature averaging 58.8° F. and adults of *L. hirsuta* emerge in 46 to 195 days when held at this same temperature.

Experimental evidence indicates that puparia of both species of quail Hippoboscidae may be kept for long periods of time at fairly low outdoor temperatures without deleterious effects. Experiments with puparia of *S. impressa* showed that they may be kept in the puparial state for at least 358 days. Adult *L. hirsuta* emerged from puparia kept outdoors for 182 to 269 days.

ACKNOWLEDGMENTS

The writer is most grateful and indebted to the following people: Dr. M. A. Stewart, under whose supervision this work was done and without whose continuing stimulus and assistance this research would not have been possible; Dr. D. P. Furman, for his many constructive and helpful suggestions pertaining to the experimental work; Dr. C. M. Herman, for suggesting this study and for his great help and guidance; Dr. J. Bequaert, for allowing the writer to use his cuts of the quail Hippoboscidae as well as for his unceasing, enthusiastic encouragement and help; Mr. and Mrs. Ian McMillan for granting permission to trap quail on their ranch and for their great help and many courtesies during this investigation. Thanks are also extended to Messrs. Ernest Twisselman, Henry Childs, H. Magini, David Selleck, Lester Hink and D. P. Furman for granting permission to trap quail on their property; to the personnel of the Disease Laboratory, California Department of Fish and Game, for their splendid cooperation at all times; to Mr. Albert Rudnick for helping the author trap quail and for his encouragement and help; and to his wife, Bernice Tarshis, to whom the author is especially indebted for many hours of loyal assistance, for helping with the trapping, and for offering many valuable suggestions throughout the entire research program.

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BOOK NOTICES

INSECTS OF HAWAII, Vol. 6, by Elwood C. Zimmerman. vii+209 pp., 106 figs. University of Hawaii Press, Honolulu. (Paper bound, 26 cm.) $4.50.

This volume is in the same format as the first five volumes of the series (1948). It is primarily devoted to the Ephemeroptera (1 sp.), Neuroptera (51 spp.), and Trichoptera (1 sp.), but there is a 25-page supplement which deals with the orders previously treated in vols. 1–5. The supplement includes records of 39 additional Hawaiian species, new data on distribution, hosts, modifications in identification keys, and corrections and other matters of such importance that notations in the previous volumes should be made to alert readers. The index covers the entire volume. Dr. Zimmerman has informed me that vols. 7 and 8 are now being printed. It should be very satisfying to entomologists to see the continuation of this outstanding, comprehensive work.

There are keys to the endopterygote orders in Hawaii; that to the larvae is adapted from one specially prepared by Dr. Fritz van Emden. The three orders treated are dealt with comprehensively, each including a bibliography of literature consulted. Relatively little information on the immature stages of these three orders in Hawaii is included, and, except for a few lowland species, scarcely anything appears to be known about the Hawaiian neuropterous larvae.

The single species each of Ephemeroptera and Trichoptera are introductions first collected in Hawaii during 1944 and 1940, respectively. The Neuroptera include two dominant families (Hemerobiidae and Chrysopidae), two apparently immigrant species (2 genera) of Coniopterygidae, and endemic Myrmeleontidae tentatively considered to represent two species and an additional subspecies of a single genus. This genus, *Eidoleon*, and the two large genera of Hemerobiidae and Chrysopidae, *Nesomicromus* and *Anomalochrysa*, show so much variation in the species that the author regards the status of some as only tentative. The characters have been illustrated fully, and the frank and full discussions are very clear. Dr. Zimmerman studied the original specimens described by Perkins, as well as material since accumulated, but especially in *Anomalochrysa*, which is comparable in its complexity to large endemic genera of other groups (i. e., in crickets and psocids), variability causes many supposed specific differences to break down when series are examined. Unfortunately, the majority of species are rare in collections, in fact nothing is known of the endemic Neuroptera of the leeward (smaller westward) islands of the Hawaiian chain.

Specialists and those entomologists interested in evolution and the development of insular faunas will benefit from Zimmerman's discussion of the genera *Pseudopsectra* and *Nesothauma*, both containing wonderfully modified, flightless species. The 19 species placed in *Nesomicromus* range from those with deeply sinuous wing margins to those whose wings have normal convex margins, and Zimmerman discusses at length the evident close relationships which warrant the congeneric status of the species which in superficial appearance seem generically distinct. Because of the variability of characters which often have been considered of generic rank in the past, Zimmerman places *Eumicromus* as a new synonym of *Nesomicromus*. The previous synonymy of *Eumicromus* under *Micromus* by Carpenter (Proc. Amer. Acad. Arts Sci. 74: 245, 1940), though not mentioned by Zimmerman, supports his contention that the hemerobiid genera need revision from a world standpoint.

An interesting fact is that originally there were no aphids in Hawaii, and especially in the case of Hemerobiidae Zimmerman believes that psocids made up a great part of the food for both larvae and adults. Now there are introduced aphids which are eaten in quantity by some of the Neuroptera. Unlike the traditional opinion regarding chrysopid eggs, those of only one Hawaiian species (the introduced *Chrysopa microphya*) are known to occur on stalks. Another noteworthy fact is that the late R. C. L. Perkins described most of the endemic Hemerobiidae and Chrysopidae, and Zimmerman pays warm tribute to the completeness of Perkins' collecting and the judgment shown in his pioneer monographic work on the Hawaiian Neuroptera.

Ashley B. Gurney.

DIE LARVALSYSTEMATIK DER BLATTWESPEN (Tenthredinoidea und Megalodontoidea), by Herbert Lorenz and Manfred Kraus. Abhandlungen zur Larvalsystematik der Insecten, No. 1, Academie Verlag, Berlin. vii+339 pp., 435 figs., bibliography, index. 1957. 38 DM ($9.00). Paperbound.

This volume is a manual for the identification of the European sawfly larvae, particularly those of Central Europe. It is, thus, a direct, lineal descendant of Enslin's Die Tenthredinoidea Mitteleuropas, published in parts from 1912 to 1917 as Beihefte of the Deutschen Entomologischen Zeitschrift. The latter contains no keys to the larvae, but does give brief descriptions of all the European sawfly larvae known at that time. Needless to say, Enslin's admirable work has long been out of print, and the original edition was quite small. (The last time I saw it listed in a second-hand book catalog the price was $35.00.)

Lorenz and Kraus, who have not published previously on the Symphyta, have here produced a volume which will be most useful in the identification of Palearctic sawfly larvae. The authors have confined themselves to sawfly larvae in the strict sense, not covering the xyelids, horn-tails, cephids, nor orussids. They have followed Benson's classification of the adults. Many of the larval characters which Lorenz and Krauss employ have, inevitably, come from Yuasa's (1922) classification of the Nearctic sawfly larvae.

After a minimum of introductory matter, the authors plunge into the keys, descriptions, and illustrations of the 462 species included in this manual. They clearly differentiate between treatments based on their own study of larval material, and information compiled from the literature. The volume abounds in bold, clear illustrations. Under each species a description of the larva is given, along with information about the host plants. Not only are the host plants listed, but the part of the plant attacked is also noted, where known. Information about the eggs is likewise included, along with other life-history or taxonomic notes, when available.

The work concludes with a comparison of the classifications that have been made, based on adults or larvae of the sawflies. This volume also has an excellent food-plant list.

B. D. Burks.

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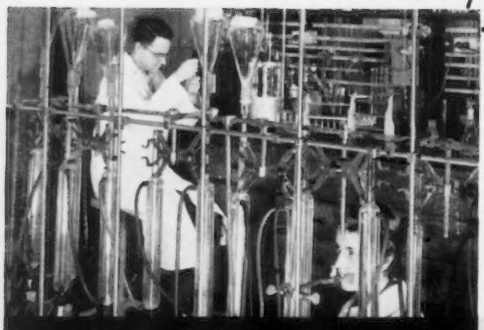

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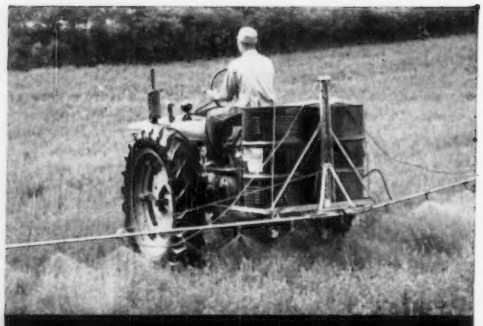

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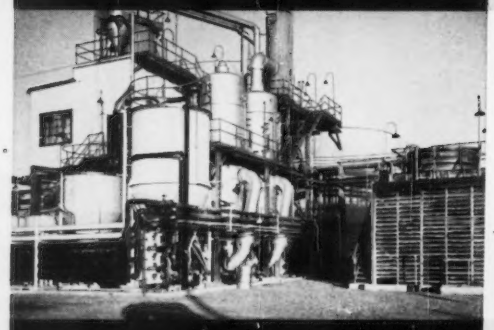

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